OCCUPATION, DISPERSAL, AND ECONOMIC IMPACT OF MAJOR INVASIVE PLANT SPECIES IN SOUTHERN U.S. FORESTS

A Dissertation

by

HSIAO-HSUAN WANG

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2009

Major Subject: Forestry

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Major Subject: Forestry

ABSTRACT

Occupation, Dispersal, and Economic Impact of Major Invasive Plant Species in Southern U.S. Forests. (December 2009)

Hsiao-Hsuan Wang, B.A., National Taiwan University;

M.S., National Taiwan University

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Invasive alien plants have impacted southern U.S. forests. This study focuses on quantifying current distribution, rate of dispersals, and economic losses caused by four major invaders — Chinese tallow (*Triadica sebifera* (L.) Small), Chinese Privet (*Ligustrum sinense* Lour.), European Privet (*Ligustrum vulgare* L.), and Japanese Honeysuckle (*Lonicera japonica* Thunb.). Using data from USDA Forest Service's Forest Inventory and Analysis (FIA), National Oceanic and Atmospheric Administration (NOAA), and USGS Land Use and Land Cover (LULC), I first used logistic regressions to build occupation models for these four species. Second, I used VB.NET© (Microsoft, 2003) and Environment System Research Institute (ESRI) Arc View® 9.2 Geographical Information System (GIS) to model spatially explicit dispersal dynamics of these species. Finally, I evaluated economic losses associated with these invasions. The results of occupation models showed that landscape features, climatic conditions, forest and site conditions, forest management activities and disturbances, and forest ownership have statistically significant impacts on current distributions of all four species. The

results of dispersal models showed that invasions of Chinese tallow, Chinese and European privets, and Japanese honeysuckle will be likely to appear on approximately 6.65 million acres of forest land in East Texas and Louisiana, 3.81 million acres in Mississippi and Alabama, and 12.55 million acres in Mississippi and Alabama, respectively, during the next 20 years. The estimated timber losses resulting from the invasion with no control for the next 20 years at 5% discount rate is 518 million dollars for Chinese tallow, 2.72 billion dollars for Chinese and European privets, and 11.05 billion dollars for Japanese honeysuckle. From an economic point of view, it would be most cost effective to execute high intensity control for these invasive species. Based on these findings, strategies for monitoring and mitigating these invasive species are proposed.

DEDICATION

I would like to dedicate this research to those I love and who love me:

Mom

Dad

Tata

William Grant

Chun-Yu Wang

Rui-Pu Wang

Ding-Yuan Wang

Elżbieta Koralewska

Sara

Gogo

Nini

John

Tomasz Koralewski

Kocham Was!!

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1. INTRODUCTION

Based on the definition by "Global Invasive Species Program" , "alien species" (non-native, non-indigenous, foreign, exotic, introduced) is a species, subspecies, or lower taxon occurring outside its normal distribution range (Koike *et al.*, 2007). However, not all introduced species become "alien invasive species". Some of introduced species fail to thrive in their new environment and extinguish naturally. Some of them survive, but without replacing native species, while others become "invasive alien species" because they threaten ecosystems, habitats or native species (SCOPE *et al.*, 2001).

There are more than 50,000 plant and animal species which have been introduced from other countries to the U.S. (Pimentel *et al.*, 2005). Some of the introduced species are beneficial; for example, species introduced as food crops and as livestock provide more than 98% of the U.S. food system. Others have been introduced for landscape restoration, biological pest control, sport, pets, and food, also with significant benefits (Pimentel *et al.*, 2000). However, some of introduced species have caused economic losses in agriculture, forestry, and several other segments of the U.S. economy, in addition to harming the environment.

Invasive alien species are spread from intentional or unintentional settings by human into the wild. Once in the wild, invasive alien species have fewer natural enemies, therefore, they may reproduce, displace native species, and impact the ecological environment. The biological invasion of the continental U.S. by alien

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This dissertation follows the style of Forest Ecology and Management.

invasive species began with European settlement almost 500 years ago and is one of the most important and challenging issues in natural resource management today (Smith and Darr, 2004).

More than 46% of the endangered species listed under the "U.S. Federal Endangered Species Act" are affected by alien invasive species (Pimentel *et al.*, 2000). Scientists estimate there are 3,727 plants with species of origin outside the United States (Smith and Darr, 2004). Invasive species can cause an irreversible change, and threaten native biological diversity (Groombridge and Jenkins, 2000; McNeely *et al.*, 2001). Biological invasions also have significant economic consequences. They have caused major environmental damages and losses adding up to almost $120 billion per year in the United States (Pimentel *et al.*, 2005). Unfortunately, the risk of introducing invasive species has increased by expanding world trade and travel during the last century (Heywood, 1995; Smith and Darr, 2004).

1.1. Problem

Southern U.S. — which includes Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, Oklahoma, Puerto Rico, South Carolina, Tennessee, Texas, the US Virgin Islands, and Virginia — is rich in its native biodiversity. However, its biodiversity is gradually changing. One of the main reasons for this change is the introduction of invasive alien plants. Invasive alien plants in the southern forests continued to go unchecked and unmonitored until early 2000 (Miller, 2003; Rauscher and Johnsen, 2004). Invasive alien plants infest under and beside forest

canopies and occupy small forest openings, increasingly eroding forest productivity, hindering forest use and management activities, and degrading diversity and wildlife habitat (Miller, 2003). Sometimes, they even alter the ecosystem by changing nutrient cycling, geomorphology and physical structure of the forest stand, drainage patterns and water flow, sedimentation rate, and disturbance regimes (Reichard and White, 2001).

Unfortunately, the invasion of alien plants in the region continues at an accelerating rate, and increases across the landscape with little opposition, beyond the control and reclamation measures applied by landowners and managers on individual land holdings. From PLANT Database (USDA and NRCS, 2009), it shows that four invasive alien plant species have broadly spread through most states in the Southern U.S. (Fig.1). These species are the Chinese tallow (*Triadica sebifera* (L.) Small), Chinese and European Privet (*Ligustrum sinense* Lour. and *Ligustrum vulgare* L.), and Japanese Honeysuckle (*Lonicera japonica* Thunb.).

Chinese tallow (*Triadica sebifera* (L.) Small) known as the chicken or popcorn tree, is a member of the spurge family (*Euphorbiaceae*) and is native and common in semitropical regions of southern and central China (Renne *et al.*, 2000). It has been cultivated in China for at least fourteen centuries as a seed crop and as an ornamental. It was introduced into South Carolina from China in 1776 by Benjamin Franklin (Randall and Marinelli, 1996). Because of the large amount of vegetable tallow found in the seed, the Foreign Plant Introduction Division of the U.S. Department of Agriculture promoted Chinese tallow planting in Gulf Coast states to establish a local soap and candle industry from 1920 to 1940 (Flack and Furlow, 1996; Miller, 2003). The Chinese tallow has

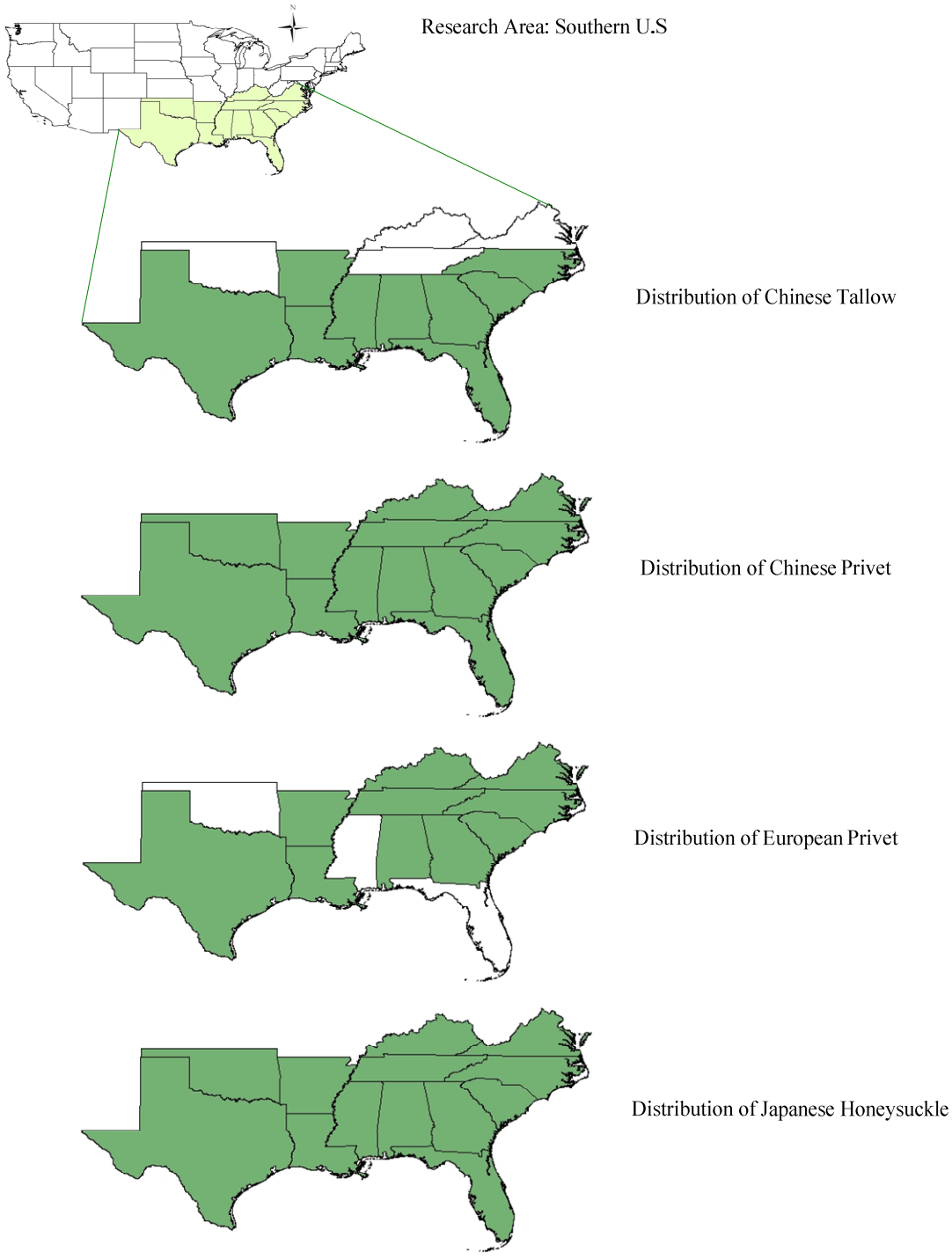


Fig. 1. Distribution of Chinese tallow tree, Chinese/European privet, and Japanese honeysuckle. The survey data for European privet were not collected in Mississippi and Florida (USDA and NRCS, 2009).

been introduced repeatedly to the U.S. as a potential oil crop species or an ornamental for its unique ornamental qualities including colorful and autumnal foliage in the last two centuries. However, it is an aggressive woody invader of wetland, coastal, and disturbed habitats, and has been shown to reduce native species diversity and richness, and alter ecosystem structure and function in natural areas. Its rapid growth and spread represents a significant threat to native forest environment in the Southern U.S (Renne *et al.*, 2000; Siemann and Rogers, 2006).

The woody plant genus *Ligustrum* represents a good example of a group of plants in which several species have become naturalized in the U.S. (Morris *et al.*, 2002). The Chinese privet (*Ligustrum sinense* Lour.) and the European privet (*Ligustrum vulgare* L.) belong to this genus. The Chinese privet is a native of China and was introduced into the U.S. in 1852, whereas, the European privet is a native of Europe and was introduced into the U.S. in the mid-1800s (Miller, 2003). Both species grow as shrubs or small trees that have been extensively cultivated for hedges and landscaping (Dirr, 1998). However, they have escaped cultivation, formed dense thickets at both the edge and interior of woods (Merriam and Feil, 2002), and dominated understory of some mesic forests throughout the south U.S. (Haragan, 1996). Privets have substantial negative impacts on native and fauna (Wilcox and Beck, 2007).

The Japanese honeysuckle (*Lonicera japonica* Thunb.) is native to Japan, Korea, and eastern China. The earliest record shows that it was introduced from China in 1806 as a horticultural specimen for Kew Gardens in New York by William Kerr. It is a valued ornamental because of its attractive and fragrant flowers. Nevertheless, Japanese

honeysuckle escaped from gardens because of its robust growth and long-flowering period (Schierenbeck, 2004). Japanese honeysuckle has replaced native flora in all forest types over a wide range of sites (Miller, 2003), and it has become naturalized in many temperate, subtropical, and tropical zones throughout the world (Schierenbeck, 2004). In the southern U.S., Japanese honeysuckle has become established and its formation of dense mats of vegetation interferes with the growth of loblolly and shortleaf pine (Skulman *et al.*, 2004).

According to the preliminary Forest Inventory and Analysis (FIA) survey results, the frequency of Chinese tallow, Chinese and European privets, and Japanese honeysuckle on all forest survey plots in the Southern U.S. are 7%, 11%, and 50%, respectively. These findings indicated that about 100 million acres of forest lands have some degree of occupation and infestation of these alien plants (Rudis *et al.*, 2006). This situation has brought some ecological and economic loss.

Because invasive alien plants have caused damages, invasion of alien species has received increasing attention. Several studies have addressed the issue at the international, regional, or national levels (McNeely *et al.*, 2001; SCOPE *et al.*, 2001). Many focus on their prevention (Miller, 2003; Koike *et al.*, 2007), physiology (Jones, 1993; Siemann and Rogers, 2007), competitions with native species (Stohlgren *et al.*, 1999; Skulman *et al.*, 2004), and management of invasion (Rauscher and Johnsen, 2004). However, there is a compelling need for quantifying their occupation and dispersals and for evaluating economic losses.

1.2. Objectives

This study focuses on quantifying occupation and dispersals, and evaluating economic losses of major invasive alien plant species — Chinese tallow (*Triadica sebifera* (L.) Small), Chinese Privet (*Ligustrum sinense* Lour.), European Privet (*Ligustrum vulgare* L.), and Japanese Honeysuckle (*Lonicera japonica* Thunb.) — in southern U.S. forest ecosystems. Specific objectives of this study include:

a) to quantify factors affecting current distributions of major invasive alien plant species on the southern U.S. forestland;

b) to derive when, where, and how much major invasive alien plant species occur on the southern U.S. forestland; and

c) to evaluate economic loss associated with the invasions of major invasive alien plant species on the southern U.S. forestland.

I will introduce these three objectives in the following three sections. In addition, I will describe how logistic regression makes habitat heterogeneity possible for spatially-explicit dispersal model and how to apply economic concepts to spatially-explicit dispersal model in order to evaluate economic loss.

2. THE OCCUPATION MODELS OF CHINESE TALLOW (*Triadica sebifera* (L.) Small), CHINESE AND EUROPEAN PRIVETS (*Ligustrum sinense* Lour. and *Ligustrum vulgare* L.), AND JAPANESE HONEYSUCKLE (*Lonicera japonica* Thunb.) ON SOUTHERN U.S. FORESTLANDS

2.1 Introduction

Based on Forest Inventory and Analysis (FIA) survey results from early 2000 until November 2008, there was a total of 42,637 forested plots in the southern U.S (Fig. 2). Thirty-three major invasive alien plant species have been detected on forestlands in this region which includes Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, North Carolina, South Carolina, Tennessee, East Texas, and Virginia. There are six tree species:

1. tree of heaven (*Ailanthus altissima* (Mill.) Swingle),
2. silktree (*Albizia julibrissin* Durazz.),
3. princesstree (*Paulownia tomentosa* (Thunb.) Siebold & Zucc. ex Steud.),
4. Chinaberrytree (*Melia azedarach* L.),
5. Chinese tallow (*Triadica sebifera* (L.) Small), and
6. Russian olive (*Elaeagnus angustifolia* L.).

Eight shrub species:

1. thorny olive (*Elaeagnus pungens* Thunb.),
2. autumn olive (*Elaeagnus umbellata* Thunb.),
3. burningbush (*Euonymus alatus* (Thunb.) Siebold),

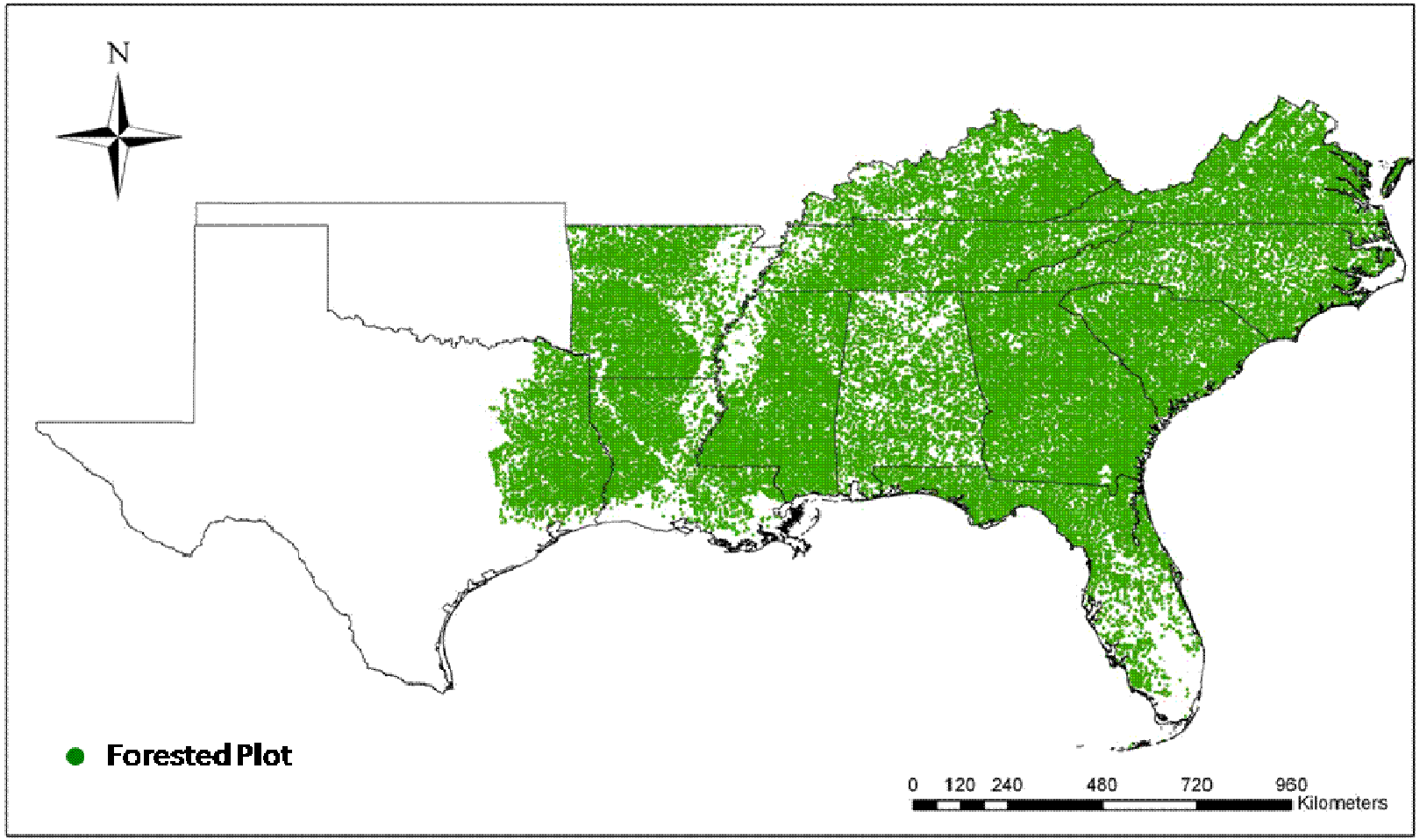


Fig. 2. Forested plots of Forest Inventory and Analysis (FIA) survey in the southern U.S.

4. thorny olive (*Elaeagnus pungens* Thunb.),
5. autumn olive (*Elaeagnus umbellata* Thunb.),
6. burningbush (*Euonymus alatus* (Thunb.) Siebold),
7. Chinese and European privets (*Ligustrum sinense* Lour. and *Ligustrum vulgare* L.),
8. Japanese privet (*Ligustrum japonicum* Thunb.),
9. bush honeysuckles (*Lonicera* L.),
10. sacred bamboo (*Nandina domestica* Thunb.), and
11. nonnative roses (*Rosa* L.).

Eight vine species:

1. Oriental bittersweet (*Celastrus orbiculatus* Thunb.),
2. air yam (*Dioscorea bulbifera* L.),
3. winter creeper (*Euonymus fortunei* (Turcz.) Hand.-Maz.),
4. English ivy (*Hedera helix* L.),
5. Japanese honeysuckle (*Lonicera japonica* Thunb.),
6. kudzu (*Pueraria montana* (Lour.) Merr. var. *lobata* (Willd.) Maesen & S. Almeida),
7. common periwinkle (*Vinca minor* L.), and
8. Chinese wisteria (*Wisteria sinensis* (Sims) DC.).

Six grasses species:

1. giant reed (*Arundo donax* L.),
2. tall fescue (*Schedonorus phoenix* (Scop.) Holub),

3. cogongrass (*Imperata cylindrica* (L.) P. Beauv.),
4. Nepalese browntop (*Microstegium vimineum* (Trin.) A. Camus),
5. Chinese silvergrass (*Miscanthus sinensis* Andersson), and
6. nonnative bamboos (*Bambusa* Schreb.).

Five major invasive ferns, forbs/herbs/other herbaceous:

1. Japanese climbing fern (*Lygodium japonicum* (Thunb.) Sw.),
2. garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande),
3. shrub lespedeza (*Lespedeza bicolor* Turcz.),
4. sericea lespedeza (*Lespedeza cuneata* (Dum. Cours.) G. Don), and
5. tropical soda apple (*Solanum viarum* Dunal)).

Among these species, Chinese tallow, Chinese and European privets, and Japanese honeysuckle represent the most aggressively invasive tree, shrub, and vine, and have invaded 2.60%, 9.64%, and 26.64% in the region's forest lands (USDA, 2008a, b). The invaded range in each FIA forested plot for Chinese tallow, Chinese and European privets, and Japanese honeysuckle could reach to 75.45%, 95.45%, and 95.45% (USDA, 2008a, b) (Table 1). This is a severe situation in the southern U.S. Because the affected area is expanding and these invasive alien plant species have great growing and reproductive attributes, there is an urgent need to develop effective mitigation plans. However, developing these plans requires more detailed information. Thus, I have developed three objectives to achieve this goal (Section 1.2). The objective of this section is to identify and analyze the major landscape features for the invasions of these four species on the southern U.S forest lands.

Table 1. Chinese tallow, Chinese and European privets, and Japanese honeysuckle forestland invasions in the southern U.S. (USDA, 2008a).

State	Number of total forested plot	Chinese tallow invaded plots			Chinese and European privets invaded plots			Japanese honeysuckle invaded plots		
		Number	%	Invaded range (%)	Number	%	Invaded range (%)	Number	%	Invaded range (%)
AL	2743	40	1.46	0.1125-54.2000	397	14.48	0.1125-95.4500	1100	40.12	0.1125-95.4500
AR	3549	7	0.20	0.1125- 1.3625	134	3.78	0.1125-54.2000	838	23.61	0.1125-75.4500
FL	3237	35	1.08	0.1125- 7.6125	25	0.77	0.1125-46.7000	23	0.71	0.1125-26.5875
GA	6578	24	0.36	0.1125-46.7000	539	8.20	0.1125-75.4500	1054	16.03	0.1125-95.4500
KY	3467	0	0.00	–	12	0.35	0.1125- 7.7250	678	19.56	0.1125-82.9500
LA	2615	406	15.53	0.1125-75.4500	253	9.68	0.1125-70.4500	435	16.64	0.1125-50.4500
MS	3771	128	3.40	0.1125-54.2000	1449	38.44	0.1125-95.4500	2515	66.71	0.1125-89.2000
NC	2819	0	0.00	–	322	11.42	0.1125-79.2000	755	26.78	0.1125-89.2000
SC	3091	31	1.00	0.1125-64.2000	398	12.88	0.1125-75.4500	985	31.88	0.1125-89.2000
TN	3540	0	0.00	–	164	4.63	0.1125-66.7000	937	26.47	0.1125-82.9500
TX	2394	410	17.13	0.1125-75.4500	135	5.64	0.1125-57.9500	495	20.68	0.1125-75.4500
VA	3833	0	0.00	–	186	4.85	0.1125-35.4500	1276	33.29	0.1125-82.9500
Total	41637	1081	2.60	0.1125-75.4500	4014	9.64	0.1125-95.4500	11091	26.64	0.1125-95.4500

2.2 Methods

2.2.1 Study species

This study chose Chinese tallow (*Triadica sebifera* (L.) Small), Chinese and European privets (*Ligustrum sinense* Lour. and *Ligustrum vulgare* L.), and Japanese Honeysuckle (*Lonicera japonica* Thunb.) as the study species. This is because not only they are the most aggressively invasive tree, shrub, and vine, but also they have invaded at a rate of 2.60%, 9.64%, and 26.64%, respectively, in the region's forest lands. (Table 1 and Figs. 3, 4, and 5).

The Chinese tallow (*Triadica sebifera* (L.) Small) has great reproductive ability. It can reach reproductive age in as little as three years and remain productive for 100 years (Duke, 1983). A mature tree may annually produce an average of 100,000 seeds (Jubinsky and Anderson, 1996). Besides, it grows rapidly. It was introduced to South Caroline in the late 1700s and quickly naturalized (Randall and Marinelli, 1996). Chinese tallow started spreading from South Carolina south to Florida, and west into Texas (Fig. 3). In addition to the above reasons, it also has a few advantages for displacing native plants and forming monotonic stands. First, it can tolerate shade even though it grows better under full sunlight. Seedlings have better shade than many native species (Siemann and Rogers, 2003). In addition, it has more tolerance of salinity and flooding than native species in the southern U.S (Miller, 2003). Some references also show it is allelopathic (Rua *et al.*, 2008), somewhat resistant to fire (USGS, 2000), and more tolerate to herbivory than native plants (Rogers and Siemann, 2004). Chinese tallow can spread by suckering, following cutting or burning. Seeds are eaten by birds

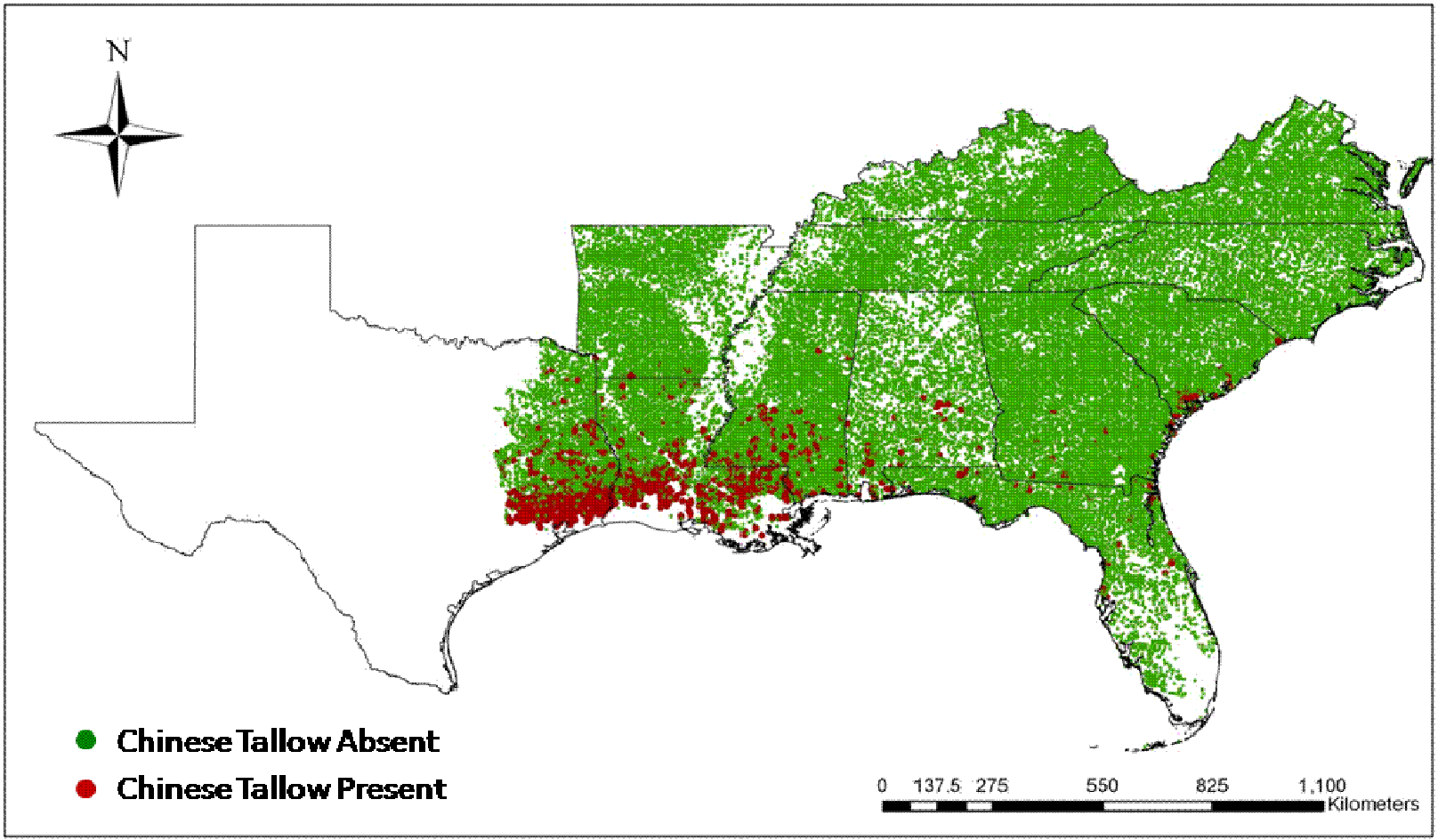


Fig. 3. Chinese tallow invasion in the southern U.S.

and float on water, and hence are easily spread by floods (Renne *et al.*, 2000; Miller, 2003). Chinese tallow grows well in subtropical to warm climates, but hardly withstands light frost (Duke, 1983).

The greatest threat posed by Chinese and European privets is large-scale ecosystem modification. They can mature rapidly, produce fruitful seeds, and reproduce vegetatively by means of root suckers. Besides, Chinese and European privets form dense thickets to invade disturbed sites, fencerows, and bottomland and upland forests in the southern U.S. (Fig. 4) (Dirr, 1998; Miller, 2003). Privets grow most rapidly in habitats with abundant sunlight, but readily invade shady forests, especially in stream floodplains (Merriam and Feil, 2002). Because of their shade tolerance and abundant regeneration, they are capable of flourishing under dense forest canopies, thereby limiting native trees regeneration, wildlife habitat, biodiversity, and recreational activities (Merriam and Feil, 2002; Harrington and Miller, 2005). These perennially shade-tolerant shrubs or small trees can grow to nine meters high, and have multiple stems and leaning-to-arching with long leafy branches (Miller, 2003). Their seeds can germinate immediately without cold stratification (Young and Young, 1992). They spread widely by abundant bird- and animal-dispersal seeds. Studies have shown their seeds and sprouts are sources of forage for songbirds, the white-tailed deer (*Odocoileus virginianus*), the white-footed mouse (*Peromyscus leucopus*), and the golden mouse (*Ochrotomys nuttalli*) (Miller, 2003; Christopher and Barrett, 2006; Rossell *et al.*, 2007; Wilcox and Beck, 2007). Land-management agencies have been alarmed with the large abundance of the privets in natural bottomland stands, difficulties in eradicate privets,

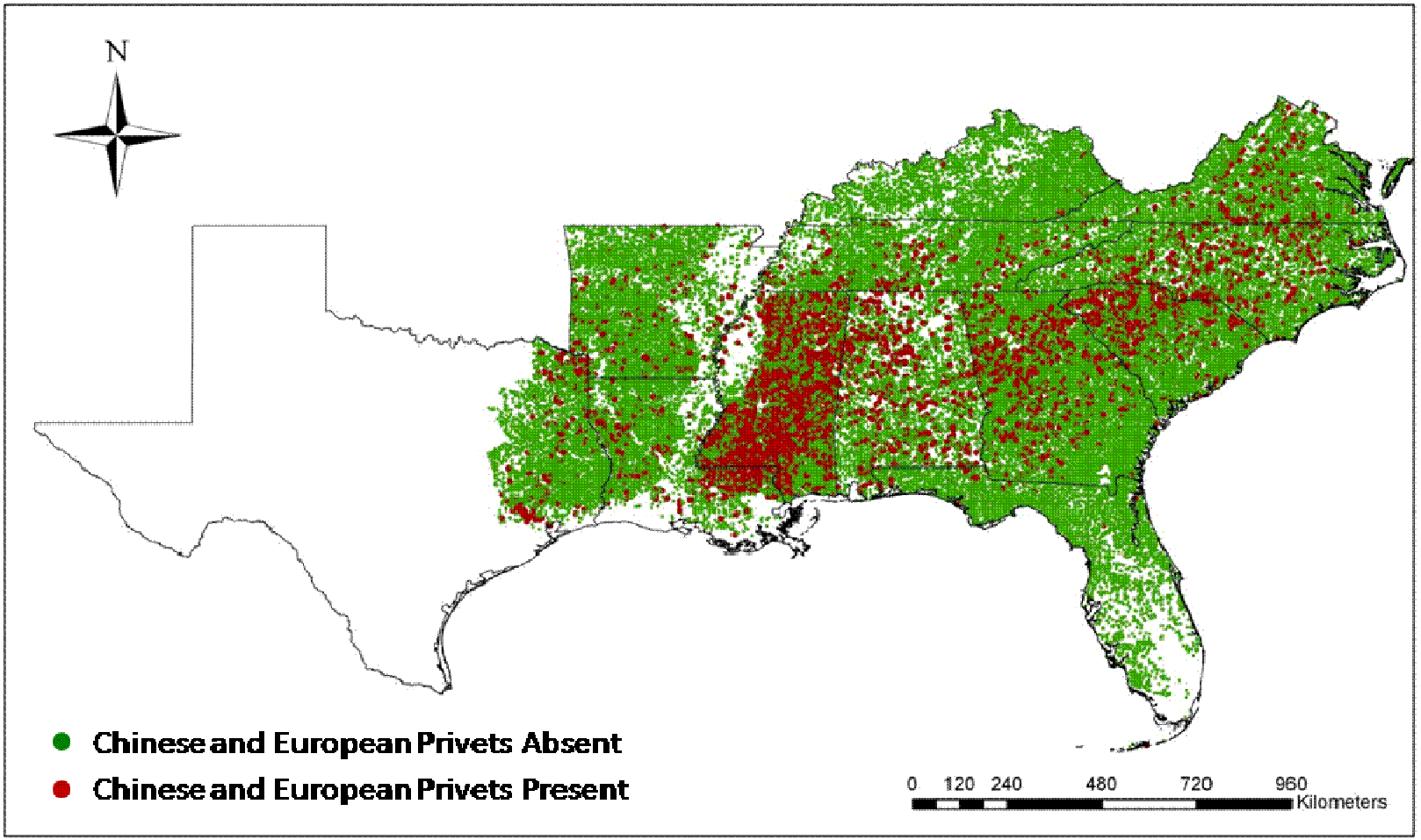


Fig. 4. Chinese and European privets invasion in the southern U.S.

and the possible loss of seedlings of native bottomland hardwood species because of competition with the privets (Brown and Pezeshki, 2000).

Japanese honeysuckle is a semi-evergreen to evergreen woody vine and can climb high and trail to 24 meters long (Miller, 2003). The herbaceous and pubescent stems quickly become densely tangled during growth. Japanese honeysuckle matures to woody and non-pubescent, eventually developing a shredded and peeling bark (Schierenbeck, 2004). Japanese honeysuckle branches and often forms arbors in forest canopies or covers the ground surface under canopies and forms long woody rhizomes that sprout frequently (Hardt, 1986). Japanese honeysuckle is the most commonly occurring invasive plant, overwhelming and replacing native flora in all forest types over a wide range of sites (Cain, 1992; Miller, 2003; Skulman *et al.*, 2004). Japanese honeysuckle can grow in full shade but prefers full sun. Japanese honeysuckle occurs as dense infestations along forest margins and right-of-ways, as well as, under dense canopies and arbors high in canopies (Miller, 2003). In addition, Japanese honeysuckle responds well to the light gaps provided by storm disturbance in the deciduous woodlands and floodplain forests of the southern U.S (Fig. 5) (Schierenbeck, 2004). Japanese honeysuckle persists by large woody rootstocks and spreads by rooting at vine nodes, ornamental cultivation, planting for wildlife forage, bank stabilization, and animal-dispersed seeds (Miller, 2003; Schierenbeck, 2004). Japanese honeysuckle fruits have been observed being eaten by wild turkeys (*Meleagris gallopavo*), bobwhites (*Colinus virginianus*), mockingbirds (*Mimus polyglottos*), white-throated sparrows (*Zonotrichia albicollis*), white-crowned sparrows (*Zonotrichia leucophrys*), slate-colored

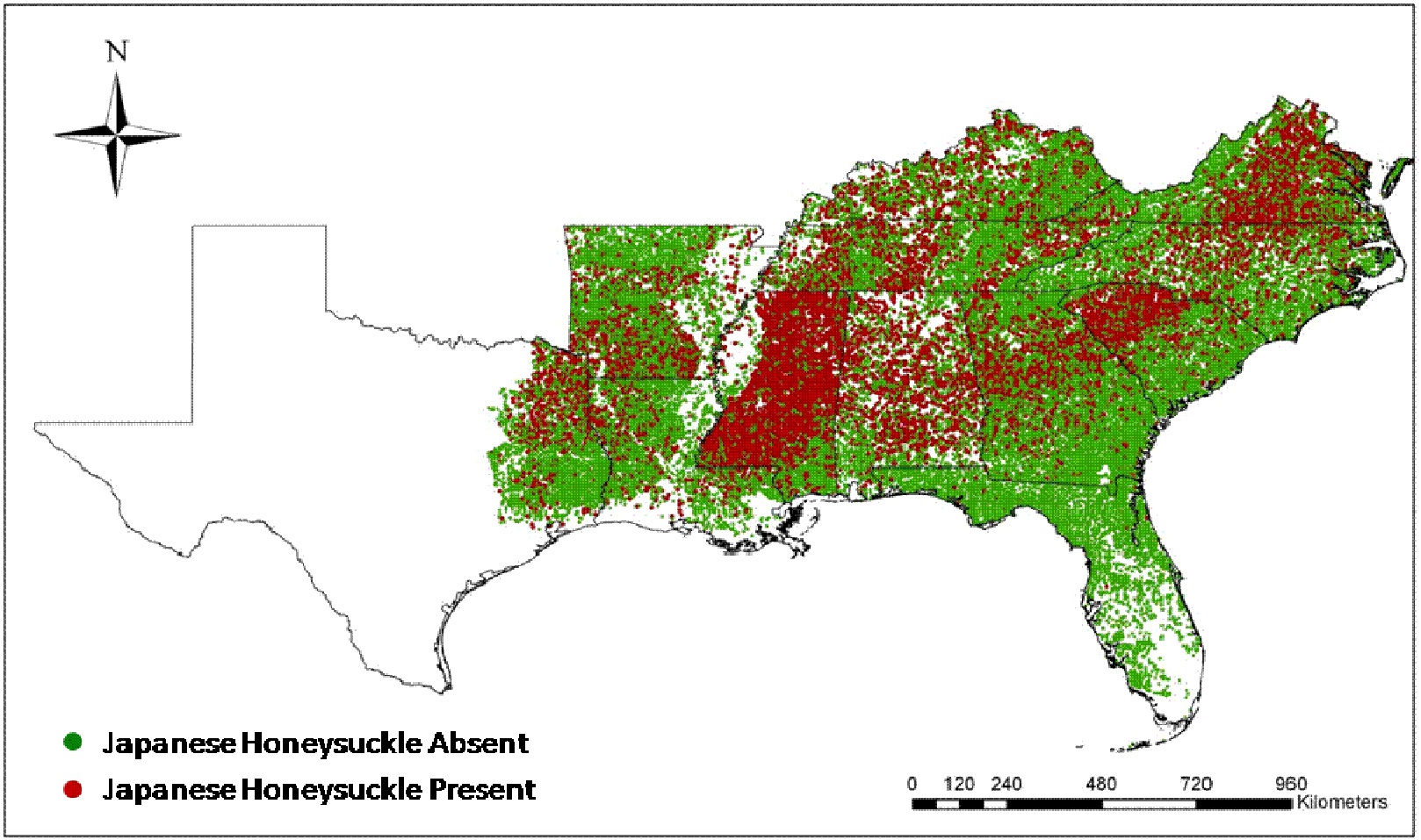


Fig. 5. Japanese honeysuckle invasion in the southern U.S

juncos (*Junco hyemalis*), American robins (*Turdus migratorius*), purple finches (*Carpodacus purpureus*), goldfinches (*Carduelis tristis*), bluebirds (*Sialia*), pine grosbeaks (Pinicola enucleator), hermit thrushes (*Catharus guttatus*), house finches (*Carpodacus mexicanus*), and white-tailed deer (*Odocoileus virginianus*) (Sheldon and Causey, 1974; Schierenbeck, 2004).

2.2.2 Study area and data sources

This study area is the southern United States, one of the most productive forest regions in the country and the world. The 534 million acres of forest resources in 13 southern states supply 62% of timber in the U.S. along with a variety of ecological services including biodiversity, wildlife habitats, water protection, and recreational resources (Merriam and Feil, 2002; Tilman *et al.*, 2002; Smith *et al.*, 2004; Battaglia *et al.*, 2007). However, invasive alien plant species have invaded under and beside forests and occupied small forest openings, increasingly eroded forest productivity, replaced native forest species, hindered forest use and management activities, rapidly accumulated biomass that increases the risk of wildfire, and degraded diversity and wildlife habitat (Miller, 2003). To manage invasive alien plant species effectively, the U.S. Department of Agriculture (USDA) Forest Service's Forest Inventory and Analysis (FIA) program of the U.S. Forest Service's Southern Research Station started conducting a national forest resource survey that provides a means of studying the problem of plant invasions in forest land in early 2000 (Rudis *et al.*, 2006). The invasive plant survey supplements traditional forest resource inventories on a 5-km grid of forest land by

Federal and state forest resource survey crews. This survey eventually samples all forests and ownerships in the 13 Southern States (Rudis *et al.*, 2006). The survey is constructed on a state-by-state basis with a plan to survey one-fifth of each state's plots annually, and thereafter on a continuing cycle. At present, preliminary analyses for frequency and severity are available for 12 states (80%-100% completed cycle), while surveys have not started in Oklahoma (Table 2).

Data used in this study were primarily drawn from two FIA datasets—the Non-native Invasive Plants dataset and the traditional FIA dataset (USDA, 2008a, b). The presence of Chinese tallow, Chinese and European privets, and Japanese honeysuckle in all plots were derived from the Non-native Invasive Plants dataset. The traditional FIA dataset provided information on stand characteristics, site conditions, management activities, and disturbances. The two sets of data were merged using FIA plot identification numbers. The data contained 41,630 plots.

Because temperature may be a critical variable in limiting or promoting species invasion, it is the need to include temperature information in this study area (Spittlehouse and Stathers, 1990; Simberloff, 2000; Pattison and Mack, 2008). Hence, climate data were derived from the National Oceanic and Atmospheric Administration (NOAA, 2008). Temperature information taken from NOAA was aligned with FIA data according to the longitudes and latitudes of FIA subplots.

Table 2. Forest Inventory and Analysis (FIA) program in the southern U.S. (USDA, 2008a).

State	Completed Cycle	New Cycle
Alabama	2001-2005 (100%)	2006-2007 (40%)
Arkansas	2002-2005 (100%)	2006-2007 (50%)
Florida	2003-2006 (80%)	N/A
Georgia	2001-2004 (100%)	2005-2007 (75%)
Kentucky	2001-2004 (100%)	2005-2006 (50%)
Louisiana	2001-2005 (100%)	N/A
Mississippi	Periodic (100%)	N/A
North Carolina	2003-2006 (80%)	N/A
Oklahoma	Periodic (0%)	N/A
South Carolina	2002-2006 (100%)	N/A
Tennessee	2001-2004 (100%)	2005-2006(75%)
Texas	2001-2003 (100%)	2004-2007 (80%)
Virginia	2002-2007 (100%)	N/A

2.2.3 Logistic regression model

Logistic regression is commonly used in different fields such as education, psychology, environmental science, biology, etc (Preece *et al.*, 2007; Quesada-Moraga *et al.*, 2007; Bondell, 2008) Logistic regression explores the relationship between a categorical output and a set of explanatory variables.

Consider the general logistic regression model with k explanatory variables, x_1, x_2, …, x_k, which are quantitative. For a binary response Y, $P(Y=1)$ denotes the "success" probability at value x_i. The probability is the parameter for the binomial distribution. The logistic regression model has linear form for the *logit* of this probability. The model for the log odds is:

$$\text{Logit}[P(Y=1)] = \log\left[\frac{P(Y=1)}{1-P(Y=1)}\right] = \alpha + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_k x_k$$

The parameter β_k refers to the effect of x_k on the log odds that $Y=1$, controlling the other x's, the formula implies that $P(Y=1)$ increases or decreases as an S-shaped function of x_k (Agresti, 2007).

This study applied the logistic regression method and modeled the probability that a susceptible plot became invaded as a function of selected landscape features (Preece et al., 2007). Because a "susceptible plot" was defined as one where Chinese tallow, Chinese and European privets, and Japanese honeysuckle were absent, invasion probability was assumed to be a nonlinear function of the landscape features.

The probability that a susceptible plot i becomes invaded, $P_i(\text{Y=1})$, was modeled using logistic regression

$$P_i(Y=1)=\frac{\exp(\lambda_i)}{1+\exp(\lambda_i)}$$

where λ_i is related to landscape features as

$$\lambda_i=\alpha+\beta_1 x_1+\beta_2 x_2+...+\beta_k x_k .$$

In the above equations, λ_i means the success probability that each plot was invaded by Chinese tallow, Chinese and European privets, or Japanese honeysuckle at value of x_k, α is a constant, while β_k is the scaling coefficient for the landscape feature. The *k* was the number of landscape features.

Next step is to determine what should be included as the independent variables. This was accomplished by building on existing work on biological invasions as related to Chinese tallow, Chinese and European privets, and Japanese honeysuckle. Hence, this study identified, from existing literature, potential explanatory variables that might have promoted the invasion of Chinese tallow, Chinese and European privets, and Japanese honeysuckle in the southern U.S. Previous work has identified several drivers of plant invasions, including landscape features such as elevation, slope, adjacency to water bodies (Jones and McLeod, 1989; Spittlehouse and Stathers, 1990; Burns and Miller, 2004), temperature condition such as extreme minimum temperature (Pattison and Mack, 2008), forest and site condition such as stand age, site productivity, and species diversity (Wills *et al.*, 1997; Filipescu and Comeau, 2007; Lombardo *et al.*, 2007), forest management activities and disturbances such as timber harvest, site preparation, artificial regeneration, natural regeneration, distance to the nearest road, fire damage, animal damage, and wind damage (Pyšek *et al.*, 2002; Huebner and Tobin,

2006). Descriptions and measurements of these variables are shown in Table 3, and most of them were recoded from traditional FIA and NOAA datasets except species diversity (NOAA, 2008; USDA, 2008a). This study computed Shannon's species diversity, H_s,.

$$H_s = -\sum_{i=1}^{n_s} \frac{B_i}{B} \ln(\frac{B_i}{B})$$

where B and B_i are the total stand basal area and the basal area of trees of species i, n_s is the number of tree species(Wills *et al.*, 1997; Filipescu and Comeau, 2007) and applied it to see if tree species richness affected the invasion of Chinese tallow trees, Chinese and European privets, and Japanese honeysuckle.

Three empirical models one each for Chinese tallow, Chinese and European privets, and Japanese honeysuckle were estimated. To select the landscape features for the model, all independent variables entered together into a stepwise logistic regression on invasion, using a backwards elimination procedure (Trexler and Travis, 1993; Sokal and Rohlf, 1995). Statistical analyses were done using SAS 9.2 (SAS Institute Inc., 2008). To this end, the insignificant terms with the largest *p*-values were removed and the model re-estimated (Liang *et al.*, 2007). This was repeated until the Akaike information criterion (AIC) (Akaike, 1973) could not be lowered.

As in ordinary regression, strong correlations among the explanatory variables could cause problems with estimates of parameters and standard errors in logistic regression. Hence, this problem was tackled by deleting one of the correlated variables that had an extremely large standard error and an insignificant coefficient estimate to

Table 3. Descriptions and measurements of independent variables.

Variable	Value or unit of measure	Expected sign of impact	Mean or frequency
Landscape features			
Elevation	m	–	139 (-36~1524)[a]
Slope	degree	–	5.39 (0~77.5)[a]
Adjacency to water bodies	0: no	+	0: 27,940
within 300 m	1: yes		1: 6,731
Temperature condition			
Mean extreme minimum	1: $T < -23.0$	+	2: 4,268
temperature (T)	2: $-23.0 \leq T < -17.8$		3: 12,466
	3: $-17.8 \leq T < -12.2$		4: 21,097
	4: $-12.2 \leq T < -6.7$		5: 4,562
	5: $-6.7 \leq T < -1.1$		6: 239
	6: $-1.1 \leq T < 4.4$		7: 2
	7: $4.4 \leq T < 10.0$		8: 3
	8: $10.1 \leq T < 15.6$ °C		
Forest and site conditions			
Stand age	years	–	44.27 (1~184)[a]
Site productivity	1: 0-1.39	+/–	1: 139
(height-age curve	2: 1.40-3.49		2: 5,912
categories)	3: 3.50-5.94		3: 17,270
	4: 5.95-8.39		4: 12,112
	5: 8.40-11.54		5: 5,609
	6: 11.55-15.74		6: 1,483
	7: >15.74 m^3/ha/yr		7: 112
Species diversity	Shannon's species diversity	+/–	1.48 (0~3.02)[a]

Table 3 Continued

Forest management activities and disturbances			
Timber harvest[b]	0: no	+	0: 36,216
	1: yes		1: 6,421
Site preparation[b]	0: no	–	0: 41,181
	1: yes		1: 1,456
Artificial regeneration	0: no	–	0: 31,545
	1: yes		1: 11,092
Natural regeneration	0: no	+/–	0: 41,663
	1: yes		1: 974
Distance to the nearest	1: <30	–	1: 2,846
road	2: 30-91		2: 4,732
	3: 91-152		3: 4,218
	4: 152-305		4: 7,409
	5: 305-805		5: 10,424
	6: 805-1609		6: 4,339
	7: 1609-4828		7: 1,349
	8: 4828-8047		8: 119
	9: >8047 m		9: 84
Fire damage[b]	0: no	+	0: 41,551
	1: yes		1: 1,086
Animal damage[b]	0: no	+	0: 42,069
	1: yes		1: 568
Wind damage[a] (including	0: no	+	0: 41,269
hurricanes and tornados)	1: yes		1: 1,368
Others			
Forestland ownership	0: public	+/–	0: 5,349
	1: private		1: 37,288

[a] Numbers inside the parentheses are the range of the variable. [b] Nominally within the past 5 years. With damage codes, at least 25% of the trees in a stand must be damaged to warrant a 1 code.

alleviate possible collinearity (Agresti, 2007). In addition, Hosmer and Lemeshow's goodness-of-fit test was used to check for the goodness-of-fit of the model (Hosmer and Lemeshow, 2000). If *p*-value of Hosmer and Lemeshow's test is greater than 0.05, this study fails to reject the null hypothesis that there is no difference between observed and model-predicted values. In the end, classification table was used to know how successfully the model could predict. This method was used to select the best model for occupation by Chinese tallow, Chinese and European privets, and Japanese honeysuckle.

Based on the results of the logistic regression, this study developed three maps for identifying the areas in the southern U. S. that are vulnerable to invasion by Chinese tallow, Chinese and European privets, and Japanese honeysuckle. For each forested plot *i*, this study assigned a habitat quality index, HQ_i, which was numerically equal to the probability of successful invasion of Chinese tallow, Chinese and European privets, and Japanese honeysuckle calculated from the logistic regression, $P_i(Y=1)$. That is:

$$HQ_i = P_i(Y=1) = \frac{\exp(\lambda_i)}{1+\exp(\lambda_i)}$$

2.3 Results and discussion

The results of logistic regressions for Chinese tallow, Chinese and European privets, and Japanese honeysuckle using the categorical and continuous data are given in Table 4. Based on (1) the *p*-values of the estimated coefficients associated with individual independent variables, (2) Hosmer-Lemeshow test results, and (3) log likelihood ratios, these models cannot reject H_0: this is an adequate model. The

Table 4. Logistic regression results for Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions estimated with discriminated data in the southern U.S.

Variable	Model fit for Chinese tallow			Model fit for Chinese and European privets			Model fit for Japanese honeysuckle		
	Estimated coefficient	Odds ratio	P-value	Estimated coefficient	Odds ratio	P-value	Estimated coefficient	Odds ratio	P-value
Elevation	-0.0033	0.9967	<0.0001	-0.0006	0.9994	<0.0001	-0.0001	0.9999	0.0359
Slope	-0.1417	0.8679	<0.0001	-0.0359	0.9647	<0.0001	-0.0253	0.9750	<0.0001
Adjacency to water bodies within 300 m	0.5626	1.7552	<0.0001	0.3433	1.4096	<0.0001	0.2080	1.2312	<0.0001
Mean extreme minimum temperature	3.0826	21.8151	<0.0001						
Stand age	-0.0086	0.9914	<0.0001	-0.0107	0.9894	<0.0001	-0.0147	0.9854	<0.0001
Site productivity	0.2529	1.2878	<0.0001	0.3520	1.4219	<0.0001	0.2676	1.3068	<0.0001
Plant species diversity	0.3870	1.4726	<0.0001	0.3242	1.3829	<0.0001	0.3580	1.4305	<0.0001
Timber harvest	0.4005	1.4926	<0.0001	0.3550	1.4262	0.017	0.1631	1.1772	<0.0001
Site preparation				-0.3789	0.6846	0.0003	-0.6060	0.5455	<0.0001
Artificial regeneration	-0.3354	0.7151	<0.0001	-0.1359	0.8729	0.0006			
Natural regeneration				0.4433	1.5578	<0.0001			
Distance to the nearest road	-0.0851	0.9184	0.0001	-0.1119	0.8941	<0.0001	-0.0781	0.9249	<0.0001
Fire damage				-0.2739	0.7604	0.0247	-0.4229	0.6551	0.0387
Animal damage				0.4238	1.5278	0.0014	0.3991	1.4905	<0.0001
Wind damage	0.7410	2.0980	<0.0001	0.5351	1.7076	<0.0001	0.2435	1.2757	<0.0001
Land ownership	1.0848	2.9588	<0.0001	0.8710	2.3893	<0.0001	0.8025	2.2311	<0.0001
Constant	-33.8072		<0.0001	-8.9183		<0.0001	-2.8363		<0.0001
P-value of Hosmer-Lemeshow test		0.4531			0.2390			0.1900	
Log-likelihood ratio		1,241.47			11,335.41			11,419.04	
AIC		2,508.94			22,702.82			22,866.08	
Overall correct prediction		77.3%			63.7%			61.0%	
Number of observations		34,671			34,671			34,671	

percentage of correct prediction are 61% for the models fitted for Japanese honeysuckle, 64% for the model fitted for Chinese and European privets, and 77% for the model fitted for Chinese tallow (Table 4).

Based on these results, this study generated three habitat quality maps for Chinese tallow, Chinese and European privets, and Japanese honeysuckle in the forests of the southern U.S (Figs. 6, 7, and 8).

The following sections summarize and discuss the key modeling results. All discussions on statistical significance, unless otherwise specified, are based on the 5% significance level.

2.3.1 Landscape features

Slope and elevation show significant impacts on the invasions of Chinese tallow, Chinese and European privets, and Japanese honeysuckle. The sites with a low elevation or a flat slope tend to be easily invaded by Chinese tallow, Chinese and European privets, and Japanese honeysuckle. The estimated coefficients for elevation and slope in these three models are negative ($\beta < 0$). This means the odds of invasion decrease by a multiple of e^{β} for every 1-unit increase in slope or elevation, controlling the other variables. Because the odds ratios (e^{β}) of slope and elevation are less than one, a one-unit increase in elevation or slope, decreases the odds ratio of Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions. The elevation effect is consistent across all models, while slope affects Chinese tallow more than Chinese and European privets and Japanese honeysuckle. This implies that Chinese and European

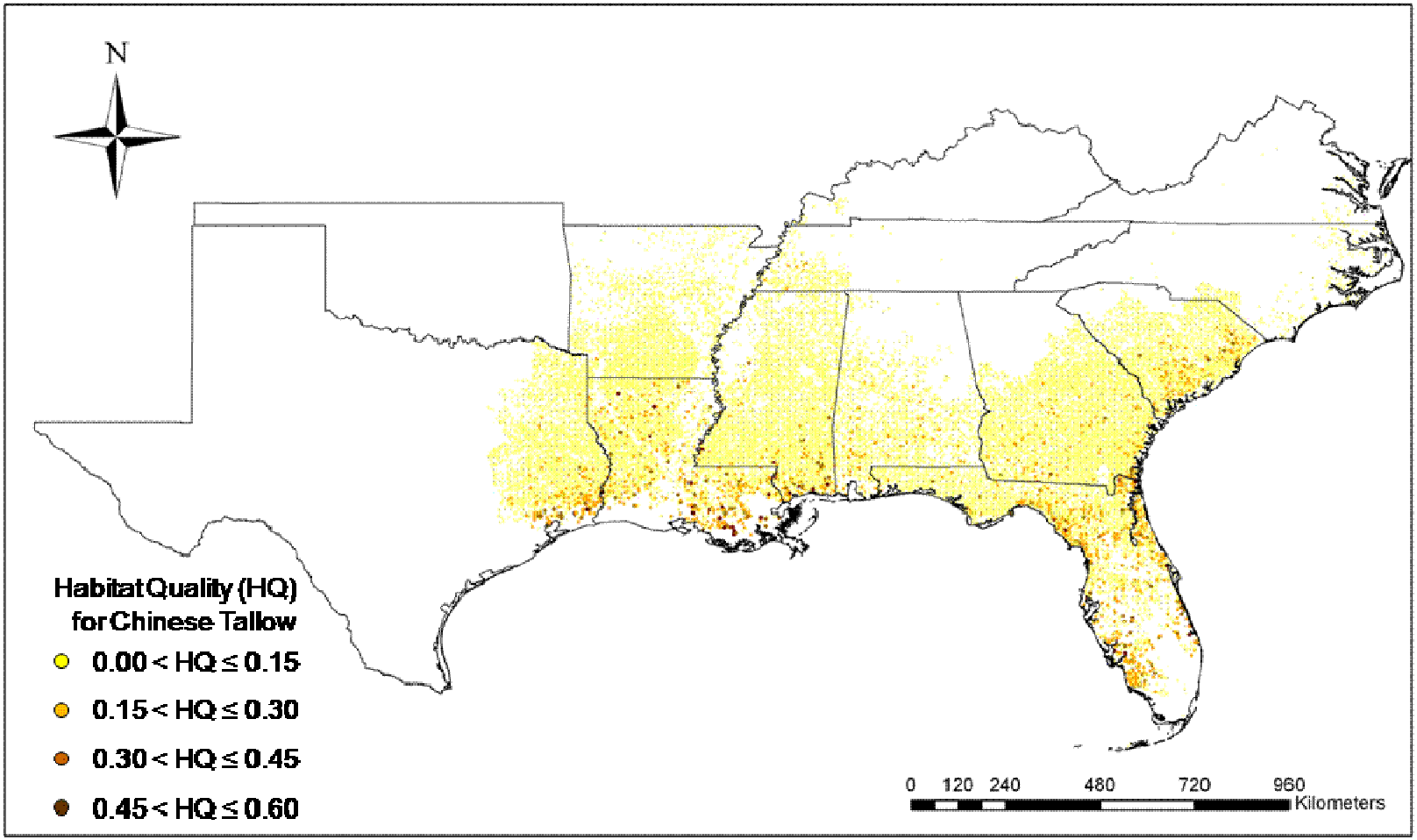


Fig. 6. Map indicating relative habitat quality for Chinese tallow in the southern U.S.

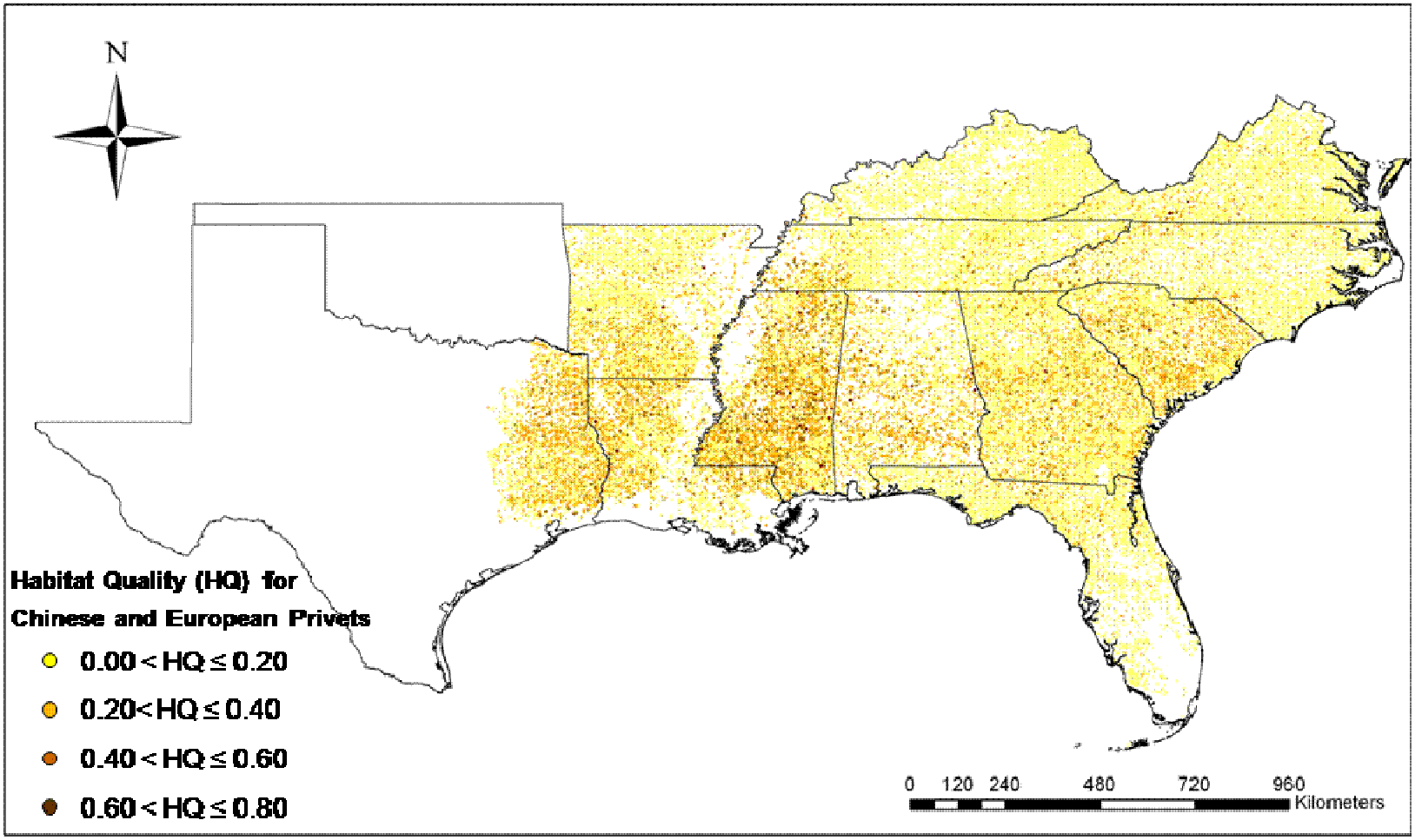


Fig. 7. Map indicating relative habitat quality for Chinese and European privets in the southern U.S.

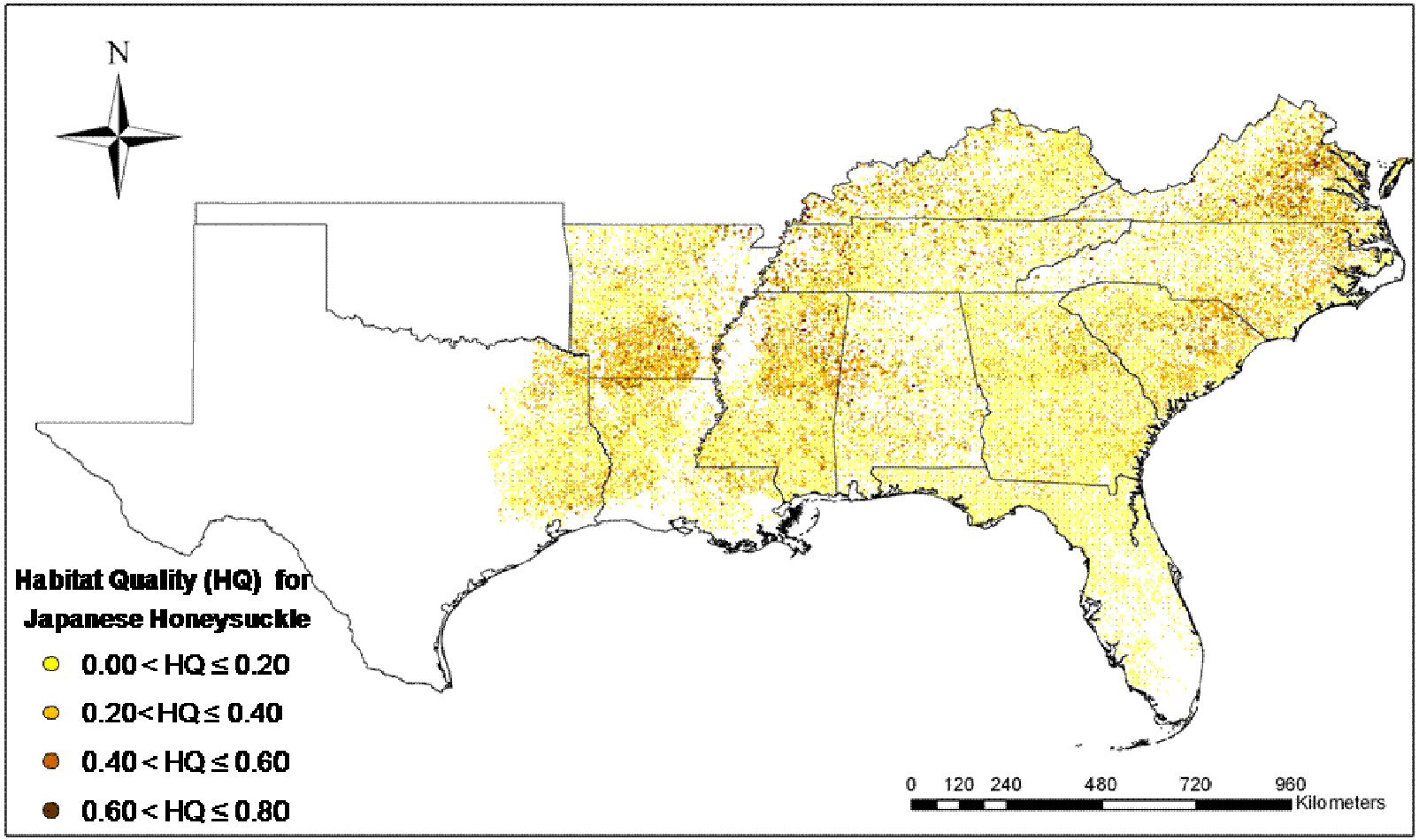


Fig. 8. Map indicating relative habitat quality for Japanese honeysuckle in the southern U.S.

privets and Japanese honeysuckle (shrubs and vines) have better climbing ability than Chinese tallow (trees), so they could adapt to steep slope better than Chinese tallow (Merriam and Feil, 2002; Miller, 2003; Schierenbeck, 2004; Loewenstein and Loewenstein, 2005).

Adjacency to water bodies (streams, swamps, bogs, marshes, ditch/canal, or flood zones) contributes positively to the occupation of Chinese tallow, Chinese and European privets, and Japanese honeysuckle, as shown in all models. The odds ratio for this predictor is relatively large (Table 4). It is because the plots near water bodies generally have high soil moisture content, favorable for the immigration, establishment and growth of Chinese tallow, Chinese and European privets, and Japanese honeysuckle (Bruce *et al.*, 1995; Jubinsky and Anderson, 1996; Merriam and Feil, 2002; Schierenbeck, 2004). It is perceived that the current North American range of Chinese tallow is restricted to the west by arid summer conditions (Schopmeyer, 1974; Bruce *et al.*, 1997).

2.3.2 Temperature condition

The mean extreme minimum temperature does not affect Chinese and European privets and Japanese honeysuckle at all, but it significantly affects the invasion of Chinese tallow. Chinese and European privets and Japanese honeysuckle already have spread broadly through most states in the southern U.S. (Fig. 1). The PLANTS database shows that Chinese privet even has spread north into Massachusetts, European privet has spread north into British Columbia and Ontario, and Japanese honeysuckle has spread

north into Ontario (USDA and NRCS, 2009). Hence, Chinese and European privets and Japanese honeysuckle have great cold tolerance and the mean extreme minimum temperature does not affect their invasion in the southern U.S. However, the mean extreme minimum temperature strongly affects the invasion of Chinese tallow. As shown in Table 4, the odds ratio for the mean extreme minimum temperature is significantly important in the model of Chinese tallow invasion. This implies that the minimum winter/spring extreme temperature serves as an important barrier to Chinese tallow northern expansion. Pattison and Mack (2008) using the CLIMEX simulation model reported similar finding. It is argued that the current North American range of Chinese tallow is restricted to the north by freezing winter temperatures (Schopmeyer, 1974; Bruce *et al.*, 1997).

According to Fourth Assessment Report (AR4) of the United Nations Intergovernmental Panel on Climate Change (IPCC), it is very likely that global average temperatures have increased since the mid-20th century due to the observed increase in greenhouse gas concentrations (Bernstein *et al.*, 2007). It is predicted that future climate changes will include further global warming. Ecosystems are seen vulnerable to climate change (Simberloff, 2000). As minimum temperature rises, the probability of Chinese tallow colonization will increase. Using the empirical model fitted with non-discriminated data, I predicted the range and probability of invasion of Chinese tallow in the study area with a warming of 1-category increase in the mean extreme minimum temperature and everything else unchanged. Both range and probability of invasion of Chinese tallow would be increased if the presumed warming occurs (Fig. 9). Chinese

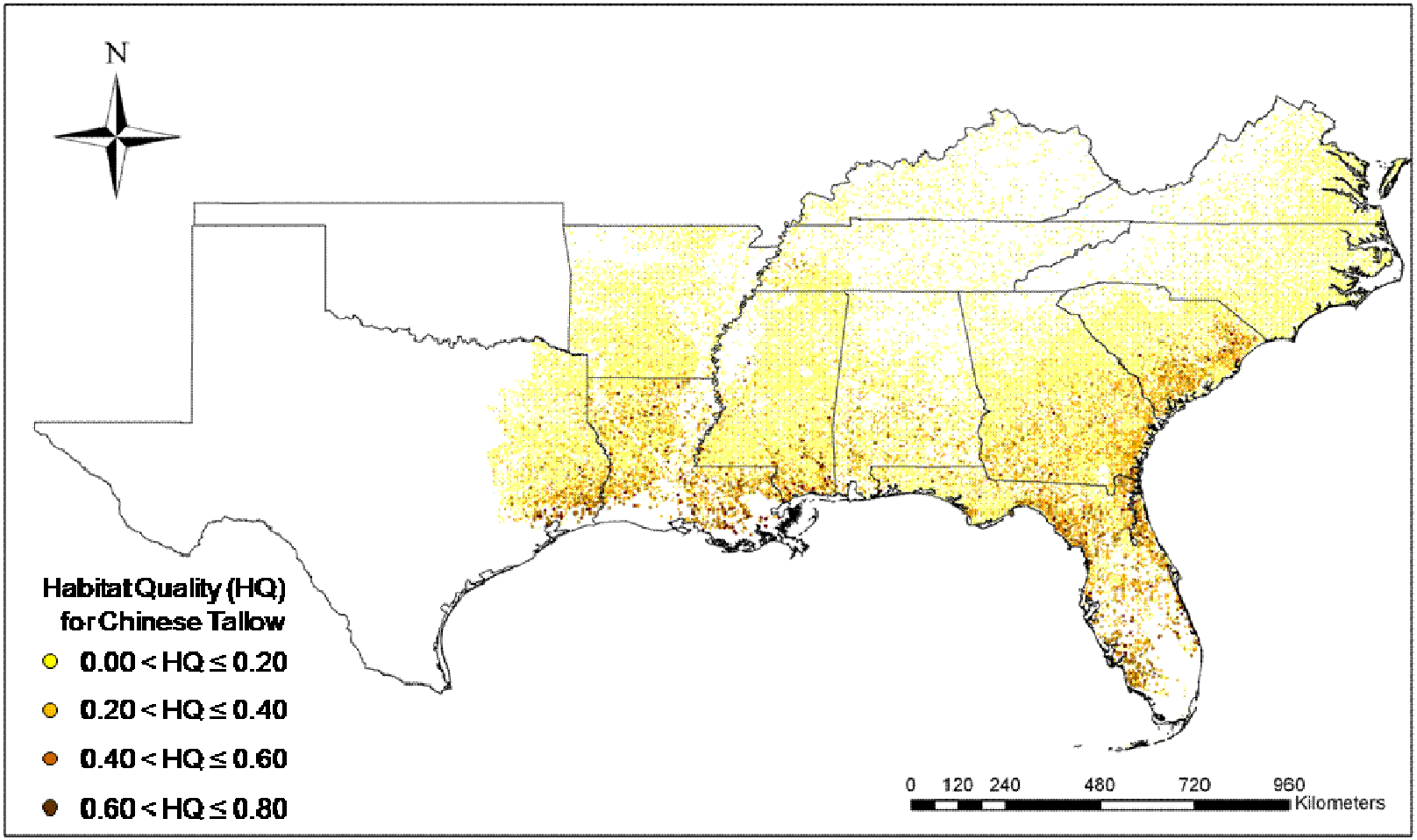


Fig. 9. Map indicating relative habitat quality for Chinese tallow with a warming of 10 ^{o}F in the southern U.S.

tallow would appear in the entire southern U.S. Hence, the predicted global warming could create a tremendous challenge for combating the geographic expansion of Chinese tallow and, if the invasions are not contained, could lead to considerable ecological and economic consequences in the southern U.S. and beyond.

2.3.3 Forest and site conditions

Forest stand age has a significant negative impact on Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions. All three models demonstrate that invasions are less likely in mature forest stands than in young ones. Because mature forest stands are saturated with trees, invasions are more difficult (Siemann and Rogers, 2006; Wilcox and Beck, 2007; Flory and Clay, 2009).

Site productivity is a classification of forest land in terms of inherent capacity to grow crops of industrial wood. It identifies the potential growth in cubicfeet/acre/year based on the culmination of mean annual increment of fully stocked natural stands (USDA, 2007a). Site productivity has a statistically significant positive effect on Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions (Table 4). This would imply that these invasive plant species prefer invading high productivity sites and they would eventually invade the land with the industrial species, such as loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*). Several references have shown that Chinese tallow, Chinese and European privet, and Japanese honeysuckle affect wood production (Merriam and Feil, 2002; Schierenbeck, 2004; Loewenstein and Loewenstein, 2005).

Tree-species diversity is, in general, a significant factor attributable to Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions. Surprisingly, Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions are positively correlated with tree-species diversity of forest stands. This may be because the plant communities invaded by these species have not yet become saturated and the invasive species are all shade tolerant (Brown and Pezeshki, 2000; Miller, 2003; Schierenbeck, 2004). Additionally, as mentioned earlier, these invasive species are more likely to occupy low elevation and productive lands that also tend to be more species diverse (Burns and Miller, 2004).

2.3.4 Forest management activities and disturbances

Several anthropogenic and natural disturbances as well as forest management activities were modeled and evaluated. Forest management activities (e.g., timber harvest, site preparation, and artificial regeneration), damages caused by wildfire, animals, and wind, and adjacency to roads showed varied impacts on invasions by Chinese tallow, Chinese and European privets, and Japanese honeysuckle.

Timber harvest generally would enhance the probability of Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions (Table 4). Harvesting creates openings and reduces competition from dominant species (Robert and Zhu, 2002), therefore enhancing the invasions of Chinese tallow, Chinese and European privets, and Japanese honeysuckle.

On the other hand, site preparation decreases the probability of Chinese and European privets, and Japanese honeysuckle invasions. Because, by definition, site preparation includes, clearing, slash burning, chopping, disking, bedding, and other practices intended to prepare a site for regeneration (USDA, 2007a), it prevents invasion by Chinese and European privets and Japanese honeysuckle.

Artificially-regenerated forest stands have a lower risk of Chinese tallow and Chinese and European privets invasions than other types of stands. These stands usually are managed more intensively than others, so artificial regeneration can prevent the invasions by these invasive plant species (Miller, 2003; Harrington and Miller, 2005). On the other hand, naturally-regenerated forest stands have a higher risk of invasions because they lack intensive management. The natural regeneration has a significant positive effect on the invasion of Chinese and European privets was indicated in Table 4.

The distance to roads is negatively related to the likelihood of Chinese tallow, Chinese and European privets, and Japanese honeysuckle colonization. Roads are an example of a widespread landscape feature that fragments habitats and creates edges with high resource availability, which act as conduits for plant dispersal (Flory and Clay, 2009). The presence of roads also can increase sun exposure and temperature, which can promote plant invasions (Davis *et al.*, 2000; Rentch *et al.*, 2005).

Fire damage shows significantly negative effects on Chinese and European privets and Japanese honeysuckle invasions. Fire damage is defined here as an area of at least 1 acre in size with a significant level of fire induced disturbance (mortality or damage to 25% of the trees) (USDA, 2007a). Some studies have shown that prescribed

burning is an efficient means of controlling invasions of Chinese and European privets and Japanese honeysuckle (Barden and Matthews, 1980; Faulkner *et al.*, 1989; DiTomaso *et al.*, 2006).

Animal damage shows significantly positive effects on Chinese and European privets and Japanese honeysuckle invasions. Animal damage is defined here as an area of at least 1 acre in size with a significant level of disturbance (mortality or damage to 25% of the trees), after caused by beaver, deer/ungulate, rabbit, and domestic animal/livestock (including grazing) (USDA, 2007a). Some references have shown that wildlife damage can be a major problem in natural tree regeneration or tree plantings (Mason *et al.*, 1999; MacGowan *et al.*, 2004). Indirectly, this situation creates opportunities for Chinese and European privets and Japanese honeysuckle invasions.

Wind-damaged stands are highly susceptible to Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions. Kyde *et al.* (2005) and Snitzer *et al.* (2005) mentioned that wind damage can facilitate the spread of invasive plant species because invasive plant species respond strongly to the increased light levels in patches of forest damaged by wind.

2.3.5 Others

Another variable that significantly affects Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions is forestland ownership. Private forestlands are far more apt to have Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions than public forestlands. The odds ratio for private ownership is

much higher than that for many other predictors included in the models. This is because public lands, in general, are more closely monitored and managed, less frequently harvested, and covered with more mature trees (Smith *et al.*, 2004). In addition, communities of invasive plant species have existed across broad areas of private land since the middle of the 19th century (Hemstrom *et al.*, 2001). Perhaps this is because there have been fewer prevention and mitigation efforts on private forestlands.

2.3.6 Spatial pattern

I only foci on how biotic and abiotic components of an ecological system affected invasions in this study. However, there were striking patterns of Japanese honeysuckle associated with Mississippi and the Piedmont in Virginia, North Carolina, South Carolina, Georgia, and Alabama in the southern U.S. (Fig. 5). Spatial patterns can determines how population move on landscape and utilize resources (Plotnick *et al.*, 1993). There are several studies have shown dispersal process interact with pattern to separate competitors in space and permit coexistence (Peacock, 1997; Johnson *et al.*, 2009b). Hence, it will be an important topic to investigate this spatial pattern of Japanese honeysuckle in the future study.

2.4 Conclusions

Logistic regression identified key drivers of Chinese tallow, Chinese and European privets, and Japanese honeysuckle invasions and estimated likelihoods of regional invasions in the southern U.S.

The occupations of Chinese tallow, Chinese and European privets, and Japanese honeysuckle are more likely to be observed on low and flat lands and those lands adjacent to water bodies and roads. The mean extreme minimum temperature strongly affects the invasion of Chinese tallow. Old or mature stands are less likely to be invaded, whereas stands with high productivity and/or high plant species diversity are more likely to be invaded. Timber harvesting tends to encourage invasions of all invasive plant species, but site preparation prevents the invasions of Chinese and European privets and Japanese honeysuckle. Artificial regeneration has negative effects on invasions of Chinese tallow and Chinese and European privets, but natural regeneration has positive effects on invasions of Chinese and European privets. Sites where at least 25 % of the trees are damaged by fire are less vulnerable to invasions of Chinese and European privets and Japanese honeysuckle. However, sites where at least 25 % of the trees are damaged by animals are more vulnerable to invasions of Chinese and European privets and Japanese honeysuckle. Generally, sites on private land where at least 25 % of the trees are damaged by wind are more vulnerable to invasions by all four invasive plant species.

The merit of this study derives from the use of broad-scale environmental and ecological survey data to identify areas vulnerable to invasion by invasive plant species. Furthermore, the analysis can be updated with the latest FIA data, and the approach can be applied to other invasive species. Logistic regression is used extensively to model invasions (Katharina *et al.*, 2007; De Valpine *et al.*, 2008), and is especially powerful for dealing with the combined influence of landscape heterogeneity and abiotic conditions

along invasion pathways (Stephenson *et al.*, 2006; Patrick *et al.*, 2007). Most importantly, this dissertation creates a potential for converting the static prediction of occupation to the dynamic projection of invasion.

3. THE DISPERSAL MODELS OF CHINESE TALLOW (*Triadica sebifera* (L.) Small), CHINESE AND EUROPEAN PRIVETS (*Ligustrum sinense* Lour. and *Ligustrum vulgare* L.), AND JAPANESE HONEYSUCKLE (*Lonicera japonica* Thunb.) ON SOUTHERN U.S. FORESTLANDS

3.1 Introduction

Invasion ecology must progress from a reactive science to a proactive science (Lodge *et al.*, 2006). This is because the increased connectivity of the global human population has amplified the frequency and effect of biological invasions (Aide and Grau, 2004). In addition, land-use and climate change interact with human transportation networks to expedite the spread of invasive species (Dukes and Mooney, 1999; Sakai *et al.*, 2001). This situation does not only increase the economic costs of control, but also causes shifts in native species richness and abundance, and alters fire regimes, water quality, and biogeochemical cycles (Strayer *et al.*, 1999; Conway *et al.*, 2002; Merriam and Feil, 2002). Hence, there is a need to adequately understand and predict the spread of invasive species to prevent and control invasive species.

An important component of prevention and control of invasive species is the ability to identify where invasions are most likely to occur initially, and to forecast where they are likely to spread. In the previous chapter, I focused on how to identify where invasions are most likely to occur (Figs. 6, 7, and 8). This was a static solution. Several studies have focused on modeling dispersal and provided dynamic prediction (Casagrandi and Gatto, 2006; Leung *et al.*, 2006; Zheng *et al.*, 2009). They were used

broadly in different fields such as pathogeny, medical, population genetics, biology, and ecology (Idnurm *et al.*, 2005; Rosenberg *et al.*, 2005; Merlo *et al.*, 2006; Vuilleumier and Metzger, 2006; Thuiller *et al.*, 2008). However, dispersal models range from very simple to extremely detailed and complex. They may involve different kinds of mathematical formulas and be applicable at different levels of biological organization. In order to identify an appropriate model, it was necessary to consider the characteristics and limits of the data and the assumptions about the dynamics of dispersal. Hence, I will describe development of a dispersal model to forecast when, where, and how much invasions are likely to spread.

3.2 Methods

3.2.1 Study area and focal species

The study area includes east Texas, Louisiana, Mississippi, and Alabama which is one of the most productive forest regions in the United States and the world. According to the FIA survey results as of the end of 2008 (USDA, 2008a), Chinese tallow, Chinese and European privets, and Japanese honeysuckle have invaded many southern states, with the most severe Chinese tallow invasions found in East Texas and Louisiana, and the most severe Chinese and European privets and Japanese honeysuckle invasions found in Mississippi and Alabama. Chinese tallow has invaded 17.13% of the forested plots sampled in East Texas and 15.53% of the plots sampled in Louisiana. Chinese and European privets have encroached on 38.44% of the plots sampled in Mississippi and 14.48% of the plots sampled in Alabama. Japanese honeysuckle has

invaded 66.71% of the plots sampled in Mississippi and 40.12% of the plots sampled in Alabama (Table 1).

3.2.2 Data sources and processing

The study of the spread of invasion has been one of the areas of biology with the greatest interplay between models and data (Andow *et al.*, 1990). The most accurate records of spread come from field mapping of invasion fronts over successive years or from time series of aerial photos (D'Antonio, 1993). However, most study data are point locations of species, such as herbaria, county weed inventories, or species lists for parks. These point data are translated into presence/absence records for geographic areas, and then sequential maps of the presence-absence data are assumed to represent the expansion of the invasion (Hastings et al., 2005). However, such data can only be used as a measure of increasing abundance, not as a measure of spread rate. The present study used the Non-native Invasive Plants dataset (USDA, 2008a) as major data source because it contains not only species lists but also the occupation percentages and locations, thus overcoming the above disadvantages. Comparing percentages and locations between two different time series can improve estimates of spread rates.

I first spatially joined the geo-referenced data from the Non-native Invasive Plants dataset, including two different time series (USDA, 2008a), the traditional FIA dataset (USDA, 2008b), and land use and land cover data (LULC) (USGS, 2009) in each of 21,850 6,000-acre (4,927m×4,927m) cells in East Texas and Louisiana and 17,360 6,000-acre cells in Alabama and Mississippi via Environment System Research Institute

(ESRI) Arc View® 9.1 Geographical Information System (GIS) (ESRI, 2005). Each cell was designed as 6,000-acre square because each sample (forested plot) is based on a national array of approximately 6,000-acre hexagons containing one permanent ground plot each, which is designated as the Federal base sample (Bechtold and Patterson, 2005) and Fishnet can only create square cells but not hexagon cells. To distinguish forest land from urban or built-up land, agricultural land, rangeland, water bodies, wetland, and barren land, I overlapped land use and land cover data (LULC) (USGS, 2009). In case where one cell contained more than one type of land use and land cover, I assigned the predominant type to the cell.

I then imported the data associated with each 6,000-acre cell into VB.NET© (Microsoft, 2003), where I developed a spatially-explicit model to forecast the spread of invasion. I created a habitat class containing instances that corresponded to each of 21,850 habitat cells in East Texas and Louisiana and 17,360 habitat cells in Alabama and Mississippi. That is, each instance contained as its attributes the spatial location (x and y coordinates), habitat quality index (HQ_i), and the old-cycle percentage land cover (N_{i,t_O}) and the new-cycle percentage land cover (N_{i,t_N}) of Chinese tallow, Chinese and European privets, or Japanese honeysuckle in the corresponding habitat cell (i).

3.2.3 Population growth model

The change in population density over time is the result of two processes: population growth and dispersal (Fig. 10). In this section, I will introduce how I constructed the single-species population growth model.

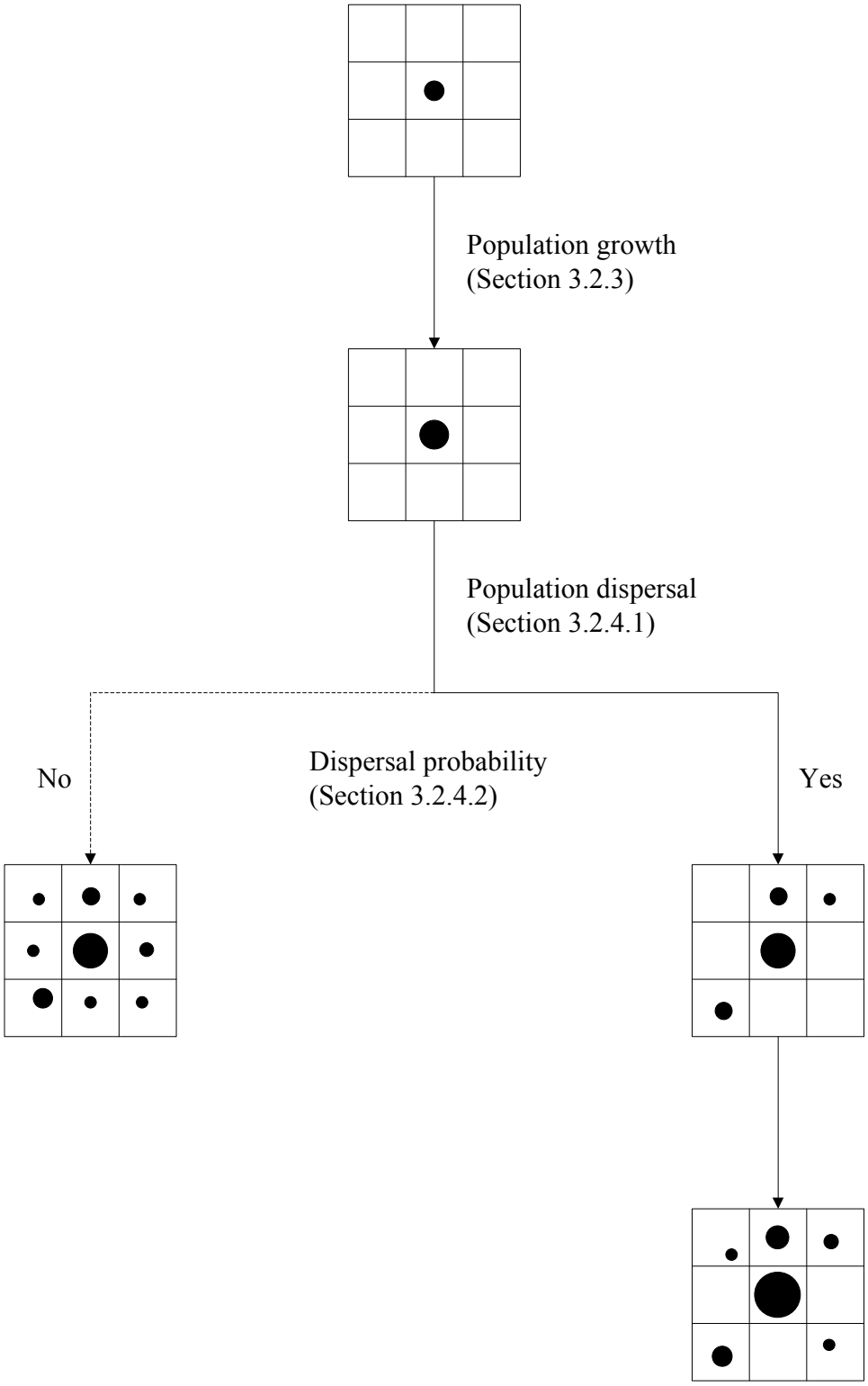


Fig. 10. Population dynamics contains population growth and population dispersal which associated with dispersal probability.

USFS Southern Research Station's Forest Inventory and Analysis (FIA) program in partnership with state forestry agencies, initiated the survey of severe plant invaders in the southern U.S. early in the year 2000. The invasive alien plant survey supplements traditional forest resource inventories and will eventually include samples from all forests in the 13 southeastern states. The survey is conducted for a 5-year period on a state-by-state basis with a plan to survey one-fifth of each state's FIA plots annually on a continuing cycle The present study used data only from those plots that had been surveyed at two different times (Table 2), and that showed an increasing invasive population. Records of the traditional FIA dataset (USDA, 2008b) indicate the plots with decreasing invasive populations were subjected to different treatments, such as invasion control and site preparation, which could bias the estimate of invasive population growth rate and thus were excluded in estimating the population dynamics of the invasions. After eliminating the plots with decreasing populations, there were 172, 83, and 146 plots used for calculating land cover growth rates for Chinese tallow, Chinese and European privets, and Japanese honeysuckle.

Exponential growth rate model and logistic growth rate model are two possible methods to calculate land cover growth rates. Because the time difference between two surveys was small, I used an exponential growth rate model to derive the maximum growth rate (r) of these invasive species (Krebs, 2009):

$$\frac{N_{t_N}}{N_{t_O}} = \exp\left[r \cdot (t_N - t_O)\right]$$

$$\Rightarrow \quad r_i = \frac{\ln\left(\frac{N_{i,t_N}}{N_{i,t_O}}\right)}{t_N - t_O} \tag{1}$$

where N_{i,t_N} is the land cover of invasion in the new cycle year in cell *i*; N_{i,t_O} is the land cover of invasion in the old cycle year in cell *i*; and $t_N - t_O$ is the time difference between old cycle and new cycle. For this calculation, the value of N_{i,t_O} cannot be zero. Hence, the numbers of qualified cells for calculating land cover growth rate for Chinese tallow, Chinese and European privets, and Japanese honeysuckle were decreased to 102, 42, and 78 respectively.

Because invasive species may not have the same rate of growth in different habitats (Klironomos, 2002; Fine *et al.*, 2006; Liang *et al.*, 2007; Zandt, 2007), particularly at leading edges of its expansion (Davis *et al.*, 2000; Jarnevich and Stohlgren, 2009), there is a need to develop a relationship between invasion cover growth rates and habitat quality. I used the available samples to parameterize the several equations relating growth rate to habitat quality: (i) $r_i = a \times \exp(b \cdot HQ_i)$, (ii) $r_i = \exp(a + b \cdot \sqrt{HQ}_i)$, (iii) $r_i = a + b \cdot HQ^2$, (iv) $r_i = a + b \cdot \ln(HQ_i)$, where r_i is the invasion cover growth rate and HQ_i is the habitat quality index of the corresponding habitat cell i. I then identified the best fit equation based on the *p*-values of the estimated coefficients (a and b) and adjusted *R*-squares.

Since population in a limited environment cannot grow exponentially forever, and because I am interested in making long-term projection of the growth of invasive

species, I incorporated the maximum growth rate (r) into a density-dependent growth model (Maynard Smith, 1971; Krebs, 2009):

$$\frac{dN_{i,t}}{dt} = r_i \times N_{i,t} \times \left(\frac{K - N_{i,t}}{K} \right) \quad (2)$$

where $N_{i,t}$ is the invasion cover in cell i at time t , K is the maximum carrying capacity, or carrying capacity, of $N_{i,t}$ (Here, I defined K equals 100%). This equation was first published by Pierre-François Verhulst in 1838 after he had read Thomas Malthus' "An Essay on the Principle of Population". Verhulst derived the logistic equation to describe the self-limiting growth of a biological population (Harris, 2001). The equation is also sometimes called the Verhulst-Pearl equation following its rediscovery by Raymond Pearl and Lowell Reed in 1920 (Bordehore *et al.*, 2003). Then, I evaluated the performance of this model by comparing the projected growth of Chinese tallow to the growth reported by Bruce *et al.* (1995). Because no data on the growth rate were available for Chinese and European privets and Japanese honeysuckle, I evaluated their projection qualitatively.

3.2.4 Dispersal models

I chose to integrate a diffusion model with an agent-based spatially-explicit simulation model to forecast the dispersal of Chinese tallow, Chinese and European privets, and Japanese honeysuckle.

Among the various types of dispersal models that I considered (Fig. 11), I discarded linear dispersal models because movement paths of real organisms rarely

resemble straight lines (Hastings *et al.*, 2005). I also discarded passive dispersal models, because they require track records with which one can identify the parents and children (Nathan *et al.*, 2008) and such data were not available for the present study.

Diffusion models appeared more promising (Fig. 11). These models estimate invasion rates from species-specific attributes related to reproduction and dispersal via two distinct approaches. The first uses independent data to estimate reproductive (growth rate, r) and dispersal (diffusion coefficient, D) parameters, and then calculates spread velocity from r and D (Skellam, 1951; Mollison, 1991). This approach, commonly referred to as reaction-diffusion models, assumes homogeneous habitats, that is, it does not account for habitat heterogeneity when deriving spread rates. The second approach uses more detailed data on population age structure to infer the velocity of dispersal, and to back-estimate the other model parameters (Bosch *et al.*, 1992). This approach assumes that movement and reproduction occur at a specific age (Bosch *et al.*, 1992), and requires long-term observational data to estimate age structure. Both approaches have been used to predict spread velocity for a variety of terrestrial and aquatic animals, some diseases, and some aquatic plants. However, neither has been applied to terrestrial plants, primarily due to their longevity and the lack of long-term data (Holmes *et al.*, 1994; Ovaskainen, 2004; Zheng *et al.*, 2009). The data used for the present study contained inventory records from the same plots at two different times, with the second sample from each plot collected approximately five years after the first. Thus, although the data did not include records on marked individuals, they did meet the basic requirements for the diffusion models. However, neither of these two kinds of

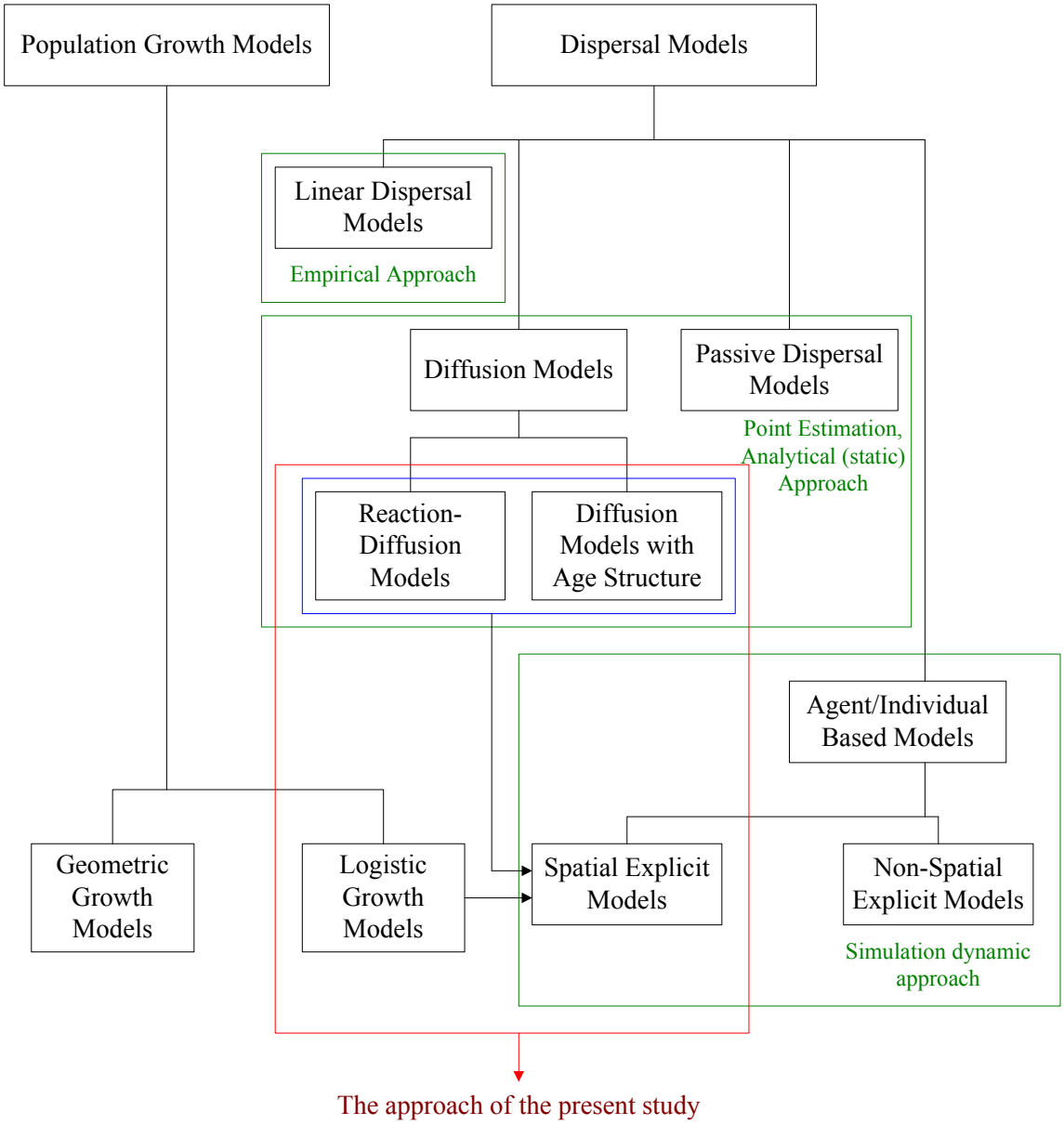


Fig. 11. The framework of dispersal models.

diffusion models is spatially explicit.

Spatially-explicit simulation models also appeared promising (Fig. 11). Ecologists interested in the movement of animals were among the pioneers in developing individual-based models and agent-based models. The focus of individual-based models is individual, its actions, and its trajectory through space and the focus of agent-based models is population and the actions and interactions of autonomous individuals (Grimm and Railsback, 2006). Thus, the idea of agent-based model fits the present study better because the data used for this study focus on invasion land cover, which can be considered as a population. The basic assumption in agent-based models is that each action by an agent during the movement process, such as whether to stop or to continue movement, or what direction to take, is a mixture of stochastic and deterministic elements. It also provides a powerful ability for integrating both movement terms and population growth terms. Agent-based movement models include spatially explicit and non-spatially explicit models (Brown *et al.*, 2004). A spatially explicit model uses geographic information as its data, on the other hand, a non-spatially explicit model does not. The spatially-explicit agent-based model also provides a rich framework for incorporating population density, space, and time. Hence, I used the ideas of spatially-explicit models for the present study because the data was constructed with spatial information and the objective of this study is to project further invasion of Chinese tallow, Chinese and European privets, and Japanese honeysuckle for 20 years.

Historically, diffusion models and spatially-explicit, agent-based models have been treated as distinct fields, although both approaches rely on the same basic

conceptual framework for modeling movement. In the following sections, I will describe how I integrated these two approaches.

3.2.4.1 Fick's diffusion equation

In addition to population growth, the change in population density from one time to the next also is the result of dispersal (Fig. 10). Here, I applied Fick's law (1855) to derive a model of dispersal. Fick's law is the classic theory of diffusion which was founded by the physiologist Adolf Fick. According to Fick's first law, the amount of transport of matter in the x distance across a unit normal area in a unit time is proportional to the gradient of the concentration of matter (So et al., 2001):

$$J_x = -D \cdot \frac{\partial N}{\partial x}$$

where J_x is the diffusion flux in dimensions of amount of substance; D is the diffusion coefficient, or diffusivity; N is the concentration of matter; and x is the distance. From Fick's first law, Fick's second law was derived, and the material balance is:

$$\frac{\partial N}{\partial t} = -\frac{\partial}{\partial x} \cdot J_x = \frac{\partial}{\partial x}\left(D \cdot \frac{\partial N}{\partial x} \right).$$

Rearranging it algebraically yields:

$$\frac{\partial N}{\partial t} = \frac{\partial}{\partial x}\left(D \cdot \frac{\partial N}{\partial x} \right) = D \cdot \frac{\partial}{\partial x} \cdot \frac{\partial N}{\partial x} = D \cdot \frac{\partial^2 N}{\partial x^2}.$$

This two-dimensional diffusion is completely analogous to the one dimensional case:

$$\frac{\partial N}{\partial t} = D \cdot \left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right). \quad (3)$$

The above equation can be solved subject to the conditions that D is a constant and initially the population in a unit area, $N_{0,0}$, is concentrated at distance $x = 0$ at time $t = 0$:

$$N_{i,d,t} = \frac{N_{i,0,0}}{4\pi D_i t} \cdot \exp\left[- \frac{\left(x^2 + y^2 \right)}{4 D_i t} \right] \quad (4)$$

where $N_{i,d,t}$ is the population size at distance $d = \sqrt{x^2 + y^2}$ from cell i at time t that is spread by the initial population, $N_{i,0,0}$; D_i is the diffusion coefficient and $D_i = \frac{V^2}{4 r_i}$; V is the speed of invasion spread (unit: m/year); and r_i is the invasion cover growth rate in cell i. Because this study can derive r_i from previous section 3.2.3, V is the only parameter that is needed further calibration.

3.2.4.2 Diffusion probability estimation

Combining equations (2) and (3) in section 3.2.3 and section 3.2.4.1 leads to Fisher's equation. Fisher's equation, also known as the Fisher-Kolmogorov equation, named after Ronald Fisher and Andrei Kolmogorov, is a partial differential equation. It combines density-dependent growth equation and Fick's diffusion equation as well as the idea of population dynamics (Hastings *et al.*, 2005):

$$\frac{dN}{dt} = r \times N \times \left(\frac{K - N}{K} \right) + D \cdot \left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right). \quad (5)$$

This equation is delineated into a deterministic one. However, deterministic methods are often used as educational models, while stochastic methods are used as practical models (Fig. 10). Okubo and Levin (2001)mentioned that nearly all biological processes are stochastic. This equation assumes that environmental conditions are constant in time and that there is no variance in the behavior of the population in certain location. Variability is a ubiquitous feature of natural systems and there are situations where variability influences both the quantitative and qualitative performance of models (Burgman *et al.*, 1993). Models take variation into account by incorporating random variation into model parameters are referred to as stochastic models (Higgins and Richardson, 1996). This study used the following method to incorporate stochasticity.

Skellam (1951) mentioned that a seed that can move in any direction in the plane is displaced through a distance ε at time t, $t+\Delta t$, $t+2\Delta t$, …. Then it must lie somewhere on a circle of radius ε centered on the position at any moment $t+\Delta t$ that it occupied at time t. Therefore, the probability, $\varphi(x, y, t+\Delta t)$, at point (x, y) at time $t+\Delta t$ is the mean of $\varphi(\xi,\eta,t)$ over all the point (ξ,η) on the circle of radius ε with center (x, y). Thus,

$$\varphi(x, y, \varepsilon, t+\Delta t) = \frac{1}{2\pi}\int_0^{2\pi} \varphi(\xi,\eta,t)d\theta .$$

Letting $\xi = x+\varepsilon\cdot\cos\theta$ and $\eta = y+\varepsilon\cdot\sin\theta$, it becomes:

$$\varphi(x, y, \varepsilon, t+\Delta t) = \frac{1}{2\pi}\int_0^{2\pi} \varphi(x+\varepsilon\cdot\cos\theta, y+\varepsilon\cdot\sin\theta, t)d\theta .$$

Expanding the left-hand side in the form of a Taylor's series and writing φ for

$\varphi(x, y, \varepsilon, t)$ gives:

$$\varphi(x, y, \varepsilon, t + \Delta t) = \varphi + \frac{\partial \varphi}{\partial t} \cdot \Delta t + \frac{1}{2!} \frac{\partial^2 \varphi}{\partial t^2} (\Delta t)^2 + \ldots$$

Similarly, expanding the right-hand side gives:

$$\frac{1}{2\pi} \int_0^{2\pi} \left[\varphi + \varepsilon \left(\cos\theta \cdot \frac{\partial \varphi}{\partial x} + \sin\theta \cdot \frac{\partial \varphi}{\partial y} \right) \right.$$

$$\left. + \frac{\varepsilon^2}{2!} \left(\cos^2\theta \cdot \frac{\partial^2 \varphi}{\partial x^2} + 2\cos\theta \sin\theta \cdot \frac{\partial^2 \varphi}{\partial x \partial y} + \sin^2\theta \cdot \frac{\partial^2 \varphi}{\partial y^2} \right) + \ldots \right] d\theta .$$

Expanding it by Taylor's theorem and noting that

$$\int_0^{2\pi} \cos\theta d\theta = \int_0^{2\pi} \sin\theta d\theta = \int_0^{2\pi} \sin\theta \cos\theta d\theta = 0 ,$$

and

$$\int_0^{2\pi} \cos^2\theta d\theta = \int_0^{2\pi} \sin^2\theta d\theta = \pi .$$

I derived

$$\varphi + \frac{\varepsilon^2}{2!} \cdot \frac{1}{2\pi} \left(\pi \cdot \frac{\partial^2 \varphi}{\partial x^2} + \pi \cdot \frac{\partial^2 \varphi}{\partial y^2} \right).$$

Then equation $\varphi(x, y, \varepsilon, t + \Delta t) = \frac{1}{2\pi} \int_0^{2\pi} \varphi(x + \varepsilon \cdot \cos\theta, y + \varepsilon \cdot \sin\theta, t) d\theta$ can be written as:

$$\frac{\partial \varphi}{\partial t} + \frac{1}{2!} \frac{\partial^2 \varphi}{\partial x^2} \Delta t + \ldots = \frac{\varepsilon^2}{4\Delta t} \left(\frac{\partial^2 \varphi}{\partial x^2} + \frac{\partial^2 \varphi}{\partial y^2} \right) + \text{negligible terms in } \frac{\varepsilon^3}{\Delta t} \text{ and higher orders.}$$

This is because powers of Δt (on the left-hand side) and $\frac{\varepsilon^3}{\Delta t}$ and higher terms (on the right-hand side) tend to zero (Pielou, 1977). Therefore:

$$\frac{\partial \varphi}{\partial t} = D \cdot \nabla^2 \varphi$$

where $D = \frac{\varepsilon^2}{4\Delta t}$.

Here, ε is the distance in the plane covered by an infinitesimal step of the particle, so that $\varepsilon^2 = (\Delta x)^2 + (\Delta y)^2$. From $D = \frac{\varepsilon^2}{4\Delta t}$, I derived $\frac{\varepsilon^2}{\Delta t} = 4D$. Symmetry considerations show that $\mathrm{var}(x) = \mathrm{var}(y) = 2Dt$. Thus, the joint distribution of x and y, the coordinates of the seed at time t, has a pdf (probability density function):

$$\varphi(x, y, \varepsilon, t) = \frac{1}{4\pi Dt} \exp\left[\frac{-(x^2 + y^2)}{4Dt}\right], \tag{6}$$

and this is the solution of $\frac{\partial \varphi}{\partial t} = D \cdot \nabla^2 \varphi$. This study applied this pdf to incorporate stochasticity. I generated a random value (9-digit decimal number) between 0 and 1, p_j, for cell *j* and I then compared this value with $\varphi_{ij}(x, y, \varepsilon, t)$. If $p_j \le \varphi_{ij}(x, y, \varepsilon, t)$, invasive species in cell *i* can spread certain amount invasion (equation (4)) to cell *j*.

3.2.5 Model simulations

The present study simulated annual increase of Chinese tallow, Chinese and European privets, and Japanese honeysuckle, respectively, using the following model:

$$N_{i,t+1} = N_{i,t} + r_i \cdot N_{i,t} \cdot \left(\frac{100 - N_{i,t}}{100}\right) + \sum_{j \neq i}^{8} \left\{ \varphi_j \cdot \frac{N_{i,t}}{4\pi D_j t} \cdot \exp\left[-\frac{(x^2 + y^2)}{4D_j t}\right] \right\} \tag{7}$$

where $N_{i,t+1}$ is the percentage of land covered by Chinese tallow, Chinese and European privet, or Japanese honeysuckle in cell i at time $t+1$, $N_{i,t}$ is the percentage of land covered by Chinese tallow, Chinese and European privet, or Japanese honeysuckle in cell i at time t, r_i is the land cover growth rate of Chinese tallow, Chinese and European privet, or Japanese honeysuckle in cell i which was calculated from section 3.2.3, φ_j is the probability that decides if Chinese tallow, Chinese and European privets, or Japanese honeysuckle could spread from any of eight adjacent cells (j) to cell i which is equation (6) and was derived from Section 3.2.4.2 , $N_{j,t}$ is the percentage of land covered by Chinese tallow, Chinese and European privet, or Japanese honeysuckle in cell j at time t, for $i \neq j$, $D_j = \frac{V_j^2}{4r_j}$, D_j is the diffusion coefficient for cell j, and V_j is the invasion velocity (m/year) for cell j. Here, I assumed that only eight adjacent cells (j) have the ability to spread seed into a center cell (i). This is because several studies have shown the maximum spread velocity hardly reaches 5,000m per year (Renne *et al.*, 2000; Clark *et al.*, 2003; Morales and Carlo, 2006) and the cell size of the present study is 4,927m×4,927m. The first term of the right hand side of equation (7) is the original percentage of land covered by Chinese tallow, Chinese and European privet, or Japanese honeysuckle in cell i at time t and it may be zero. The second term of the right hand side of equation (7) is the density-dependent (logistic) growth of Chinese tallow, Chinese and European privet, or Japanese honeysuckle in cell i at time t. If the original percentage of land cover is zero, the second term of the right hand side of

equation (7) is zero. The third term of the right hand side of equation (7) is how much invasion could spread to cell i at time t by adjacent cells.

To simulate the dispersal of Chinese tallow, Chinese and European privets, and Japanese honeysuckle, the present study hypothesized different velocities governing the probability and magnitude of invasion. To derive the appropriate the probability and magnitude, there was a need to calibrate the spreading velocity. I tested eight different dispersal velocities, including 4,927 (4,927/1), 2,463.5 (4,917/2), 1,642.33 (4,927/3), 1,231.75 (4,927/4), 985.4 (4,927/5), 821.17 (4,927/6), 703.86 (4,927/7), and 615.88 (4,927/8) (unit: m/year), in the equation (7) and let $\varphi_j = 1$ as a deterministic model. I chose these eight different dispersal velocities because I would like to check how many years will take an invasive species to invade one cell. Then, I evaluated the eight versions of the model with different dispersal velocities by comparing the spatial patterns of invasion generated by this deterministic model to the historical invasion patterns of Chinese tallow, Chinese and European privets, and Japanese honeysuckle and derived appropriate velocities.

The present study evaluated how well these eight simulated patterns matched patterns in the new-cycle data using Pearson correlation coefficient (Dutilleul's modified t-test) (Dutilleul *et al.*, 1993) and cross-Mantel test. Pearson correlation coefficient (Dutilleul's modified t-test) was used to measure the direct correlation between the observation and the prediction because it corrects the degrees of freedom according to the level of autocorrelation in the data (Dutilleul *et al.*, 1993) was used to assess the significance of the direct correlations. The spatial correlations between the changes

among given variables were evaluated using cross Mantel tests, which are Mantel tests using two variable distance matrices based on data for the observation and the prediction in the same set of locations. The cross Mantel test is used to assess the correlation between the spatial patterns. PASSAGE software (Rosenberg, 2001) was used for these tests.

Then, I calibrated the spreading velocities such that simulated and observed spatial patterns of invasion were similar and have positive values based on the *p*-value<0.05 of these tests. After deriving the appropriate spreading velocities, I applied them to calculate the associated spreading probabilities φ_j and ran the baseline simulation for the stochastic model.

Baseline simulation for stochastic models actually consists of a set of replicate, 20-year, stochastic (Monte-Carlo) simulations (Grant *et al.*, 1997). Thus, an additional consideration arose at this point - how many replicate simulations should be run. In other words, what would be an adequate sample size to detect differences in the mean number of acres invaded by Chinese tallow, Chinese and European privets, and Japanese honeysuckle, by the end of the 20-year simulations. A formula providing an estimate of an adequate sample size n when testing a two-sided hypothesis about the mean, μ, is:

$$n = \frac{\sigma^2}{\Delta^2}(z_{\alpha/2} + z_{\beta})^2 \tag{9}$$

where $n =$ number samples, $\sigma =$ true standard deviation, $\Delta =$ smallest true difference that the study desires to detect, and α and β equal Type I and Type II error probabilities (Ott and Longnecker, 2001). For the present study, I estimated σ based on

50 preliminary replicate stochastic simulations, and chose $\alpha = 0.05$ ($z_{\alpha/2} = 1.96$), $\beta = 0.01$ ($z_{\beta} = 2.326$), and $\Delta =$ 6000 acres. Hence, the sample sizes for Chinese tallow, Chinese and European privets, and Japanese honeysuckle were 175, 141, and 198.

I evaluated the several versions of the model with different appropriate dispersal velocities by comparing the spatial patterns of invasion generated by the appropriate number of replicate stochastic simulations to the historical invasion patterns of Chinese tallow, Chinese and European privets, and Japanese honeysuckle. Before comparing the simulated and observed patterns of invasion, I deleted cells that contained both old-cycle data (N_{i,t_O}) and the new-cycle data (N_{i,t_N}) and only kept cells which $N_{i,t_O} = 0$ and $N_{i,t_O} > 0$. I then used these remaining cells and Mantel's test to identify the version of the model with the dispersal velocity that generated the spatial pattern most highly significantly correlated with the observed pattern.

Finally, I projected the invasions of Chinese tallow, Chinese and European privets, and Japanese honeysuckle over the next 20 years. Usually, the timber industry harvests pine trees every 25 years and pulpwood trees every 15 years, with all aboveground plant species also being removed. Hence, the present study only projected the invasions in next 20 years by averaging 25 and 15 years. I used Fig. 12 to describe the simulation flow chart. I then exported the geo-referenced simulated data to ArcView® to visualize and analyze the spatial patterns of simulation results.

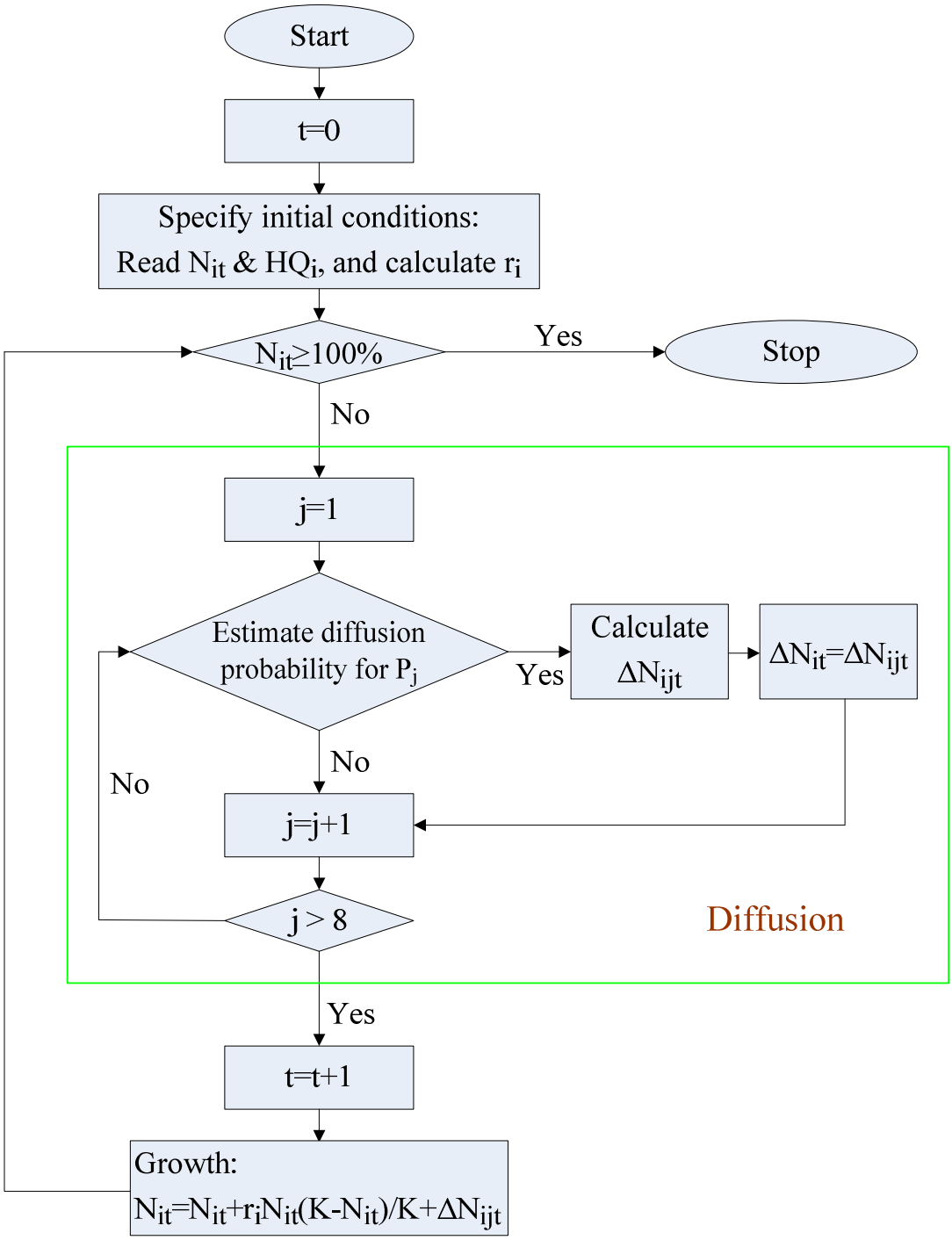


Fig. 12. Flow chart of the simulation model.

3.3 Results

3.3.1 Population growth rates

Of the four equations that I parameterized to relate growth to habitat quality (Section 3.2.3), equation (i) was the best fit equation for all invasive species (Table 5). Bruce *et al.* (1995) mentioned that if the initial population of Chinese tallow could grow in a favorable environment, this species could completely colonize its favorable environment within 30 years. Hence, I chose the lowest value in the Non-native Invasive Plants dataset (USDA, 2008a) for the initial population of Chinese tallow ($N_0 = 0.1125\%$), applied the four highest habitat quality index values, $HQ_i = 0.6622$, 0.5606, 0.4349, and 0.3298, to calculate the growth rate by equation (i), $r_i = 0.3577 \times \exp(1.0182 \cdot HQ_i)$, and derived the growth rates, $r_i = 0.5058$, 0.4561, 0.4013, and 0.3605 (% of land cover / year). Then, I applied these four growth rates to the density-dependent growth model. The result (Fig. 13) shows that Chinese tallow can start colonizing a favorable habitat when the initial population is as small as 0.1125% and then almost occupies 100% of this habitat within 30 years. Even though the adjusted *R*-square for Chinese tallow is not very high, this result implies that the growth rate equation (i) is appropriate for Chinese tallow in a favorable habitat.

Table 5. Results of parameterizing four equations relating growth rate to habitat quality for Chinese tallow, Chinese and European privets, and Japanese honeysuckle.

	Chinese tallow		Chinese and European privets		Japanese honeysuckle	
	Parameter estimate	R^2	Parameter estimate	R^2	Parameter estimate	R^2
(i) r_i [†] $= a \times \exp(b \cdot HQ_i)$ [#]	$a = 0.3577$ *		$a = 0.1359$ *		$a = 0.1455$ *	
	$b = 1.0182$ *	0.2603	$b = 0.4261$ *	0.1555	$b = 0.7533$ *	0.1617
(ii) $r_i = \exp(a + b \cdot \sqrt{HQ}_i)$	$a = -1.1563$ *		$a = -2.0914$ *		$a = -2.2389$ *	
	$b = 0.7557$ *	0.2388	$b = 0.4197$ *	0.0921	$b = 0.9947$ *	0.1568
(iii) $r_i = a + b \cdot HQ_i^2$	$a = 0.5342$ *		$a = -1.9227$ *		$a = 0.1780$ *	
	$b = 0.7088$ *	0.2572	$b = -0.2214$ *	0.0025	$b = 0.2049$ *	0.1488
(iv) $r_i = a + b \cdot \ln(HQ_i)$	$a = -2.4399$ *		$a = 0.3080$ *		$a = 0.2795$ *	
	$b = 0.5670$ *	0.2488	$b = 0.0297$ *	0.1460	$b = 0.0668$ *	0.1509

[†] r_i is the invasion cover growth rate of the corresponding habitat cell i. [#] HQ_i is the habitat quality index of the corresponding habitat cell i. * P-value < 0.01

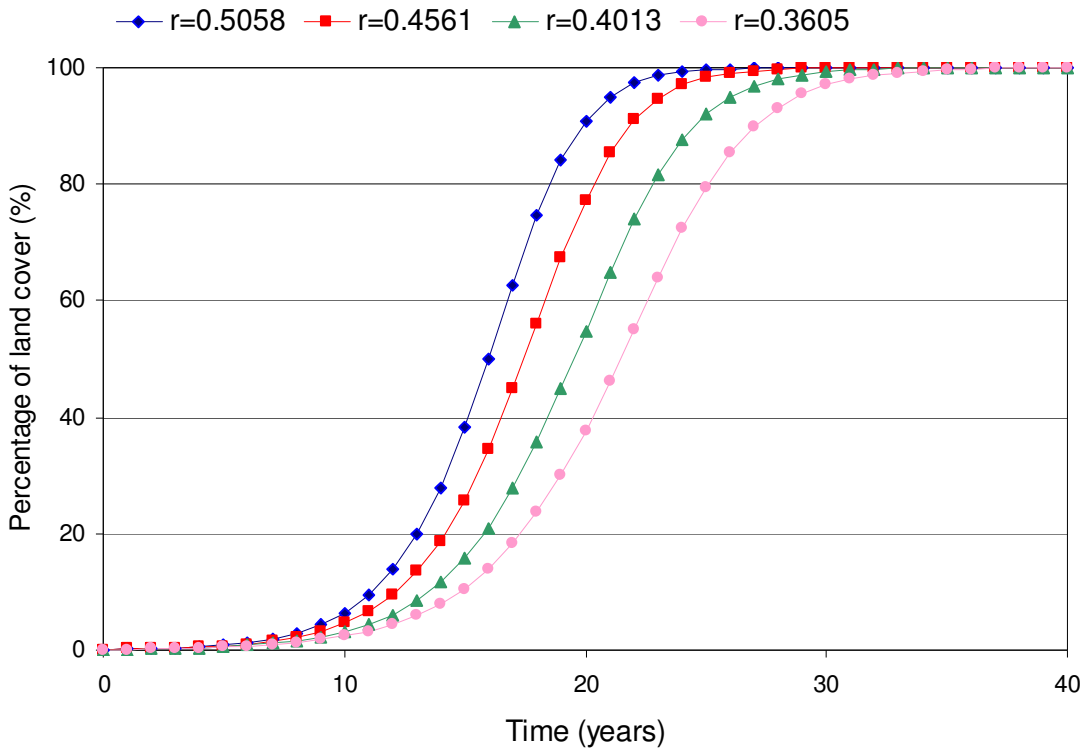


Fig. 13. The density-dependent growth for Chinese tallow.

Even though no data on growth rates were available for Chinese and European privets and Japanese honeysuckle, I still used the same approach toestimate the growth rate for Chinese and European privets and Japanese honeysuckle. The results showed Chinese and European privets and Japanese honeysuckle occupy 100% of a favorable habitat within 60 and 45 years, if the initial population is as small as 0.1125%. Usually, shrubs and vines cannot tolerate severe disturbances, such as flooding, wildfire, and herbivores (Rogers and Siemann, 2004; Reilly *et al.*, 2006; Predick and Turner, 2008). Hence, it is no surprise that these species take longer time than Chinese tallow to completely colonize a favorable habitat.

3.3.2 Velocity of dispersal

Of the eight dispersal velocities that I evaluated using the deterministic model (Section 3.2.3.4), several resulted in simulated patterns of invasion that were not statistically significantly different from the observed patterns (Table 6). Further evaluation of these velocities using the stochastic model indicated that the most appropriate velocities for Chinese tallow, Chinese and European privets, and Japanese honeysuckle were 985.40, 703.86, and 821.17 (m/year) (Table 7), based on the p-value<0.05, the positive Pearson's r (Dutilleul's modified t-test), and the positive spatial correlation (cross-Mantel's test).

Table 6. Results of direct correlation (Pearson's r with Dutilleul's modified t-test) and spatial correlation (cross-Mantel's test) comparing observed patterns of invasion for Chinese tallow, Chinese and European privets, and Japanese honeysuckle with simulated deterministic patterns generated using the eight different dispersal velocities.

Species	Chinese tallow (Sample size: 172)			
	Direct correlation		Spatial correlation	
Velocity	Person's r	*p*-value	Mantel's r	*p*-value
4927.00	0.0226	0.328	-0.0253	0.663
2463.50	0.0611	0.212	-0.0222	0.625
1642.33	0.2178	0.001	0.1644	0.001
1231.75	0.5291	0.001	0.4592	0.001
985.40	0.5378	0.001	0.4886	0.001
821.17	0.5278	0.001	0.4884	0.001
703.86	0.5277	0.001	0.4881	0.001
615.88	0.5277	0.001	0.4881	0.001
Species	Chinese and European privets (Sample size: 83)			
	Direct correlation		Spatial correlation	
Velocity	Person's r	*p*-value	Mantel's r	*p*-value
4927.00	0.0083	0.975	-0.071	0.978
2463.50	0.0055	0.931	-0.0642	0.943
1642.33	0.0331	0.886	-0.0453	0.843
1231.75	0.0412	0.611	-0.0267	0.842
985.40	0.0911	0.426	-0.0019	0.779
821.17	0.1249	0.421	0.0255	0.793
703.86	0.3117	0.001	0.2347	0.020
615.88	0.3078	0.001	0.1809	0.043
Species	Japanese honeysuckle (Sample size: 146)			
	Direct correlation		Spatial correlation	
Velocity	Person's r	*p*-value	Mantel's r	*p*-value
4927.00	0.0054	0.803	-0.0361	0.546
2463.50	0.0077	0.861	-0.0372	0.515
1642.33	0.0131	0.826	-0.0381	0.538
1231.75	0.0334	0.500	-0.0473	0.480
985.40	0.3277	0.194	-0.0178	0.587
821.17	0.5497	0.018	0.5051	0.001
703.86	0.4278	0.008	0.4260	0.001
615.88	0.4256	0.005	0.2681	0.012

Table 7. Results of direct correlation (Pearson's r with Dutilleul's modified t-test) and spatial correlation (cross-Mantel's test) comparing observed patterns of invasion for Chinese tallow, Chinese and European privets, and Japanese honeysuckle with simulated stochastic patterns generated using the eight different dispersal velocities.

Species	Chinese tallow (Sample size: 172)			
	Direct correlation		Spatial correlation	
Velocity	Person's r	*p-value*	Mantel's r	*p*-value
1642.33	0.2970	0.001	0.2034	0.001
1231.75	0.5931	0.001	0.5153	0.001
985.4	0.6458	0.001	0.5684	0.001
821.17	0.6263	0.001	0.5477	0.001
703.86	0.6259	0.001	0.5292	0.001
615.88	0.6277	0.001	0.5113	0.001
Species	Chinese and European privets (Sample size: 83)			
	Direct correlation		Spatial correlation	
Velocity	Person's r	*p-value*	Mantel's r	*p-value*
703.86	0.4685	0.001	0.3543	0.001
615.88	0.3925	0.001	0.2532	0.001
Species	Japanese honeysuckle (Sample size: 146)			
	Direct correlation		Spatial correlation	
Velocity	Person's r	*p-value*	Mantel's r	*p-value*
821.17	0.6321	0.018	0.6311	0.001
703.86	0.5113	0.008	0.5013	0.001
615.88	0.5195	0.005	0.3156	0.001

3.3.3 Simulation results

Projections of invasions in East Texas and Louisiana indicated that Chinese tallow has the potential to expand from the 0.15 million acres that it occupied in 2003 to 6.65 million acres in 2023 (Fig. 14), which represents 12.84% of all forest lands (51.77 million acres) in East Texas and Louisiana. Chinese and European privets have the potential to expand from the 0.82 million acres occupied in 2003 to 3.81 million acres in 2023 (Fig. 15), which represents 5.65% of all forest lands (67.45 million acres) in Mississippi and Alabama. Japanese honeysuckle has the potential to expand from the 2.54 million acres that it occupied in 2003 to 12.55 million acres in 2023 (Fig. 16), which represents 18.61% of all forest land in Mississippi and Alabama.

Geographically, the invasion of Chinese tallow expands toward north and colonizes the lands along the Gulf of Mexico. Chinese and European privets have been observed most forest land in the year 2003, so their invasion tends to complete colonizing the original range. The invasion by Japanese honeysuckle expands southwards and tends to complete colonizing the original range. Figs. 17 - 31 visualize the spatial invasion patterns of simulation results every five years for Chinese tallow, Chinese and European privets, and Japanese honeysuckle in the next 20 years.

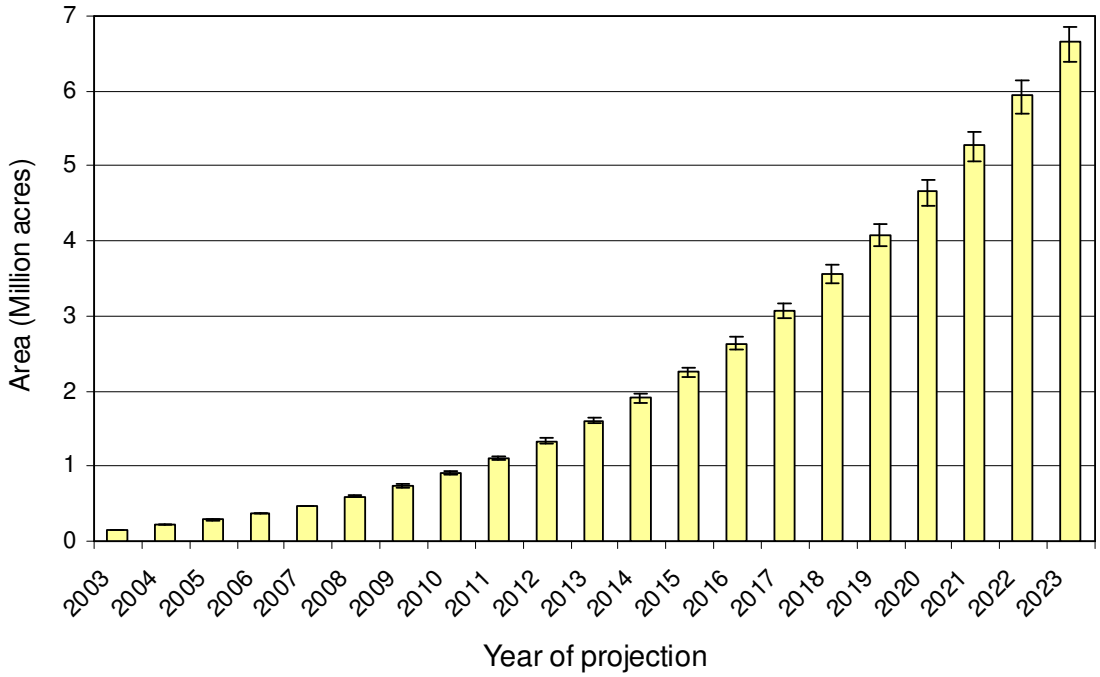


Fig. 14. Projection of the mean (vertical bars represent 95% CI) number of acres invaded by Chinese tallow in East Texas and Louisiana based on 175 stochastic (Monte-Carlo) simulations.

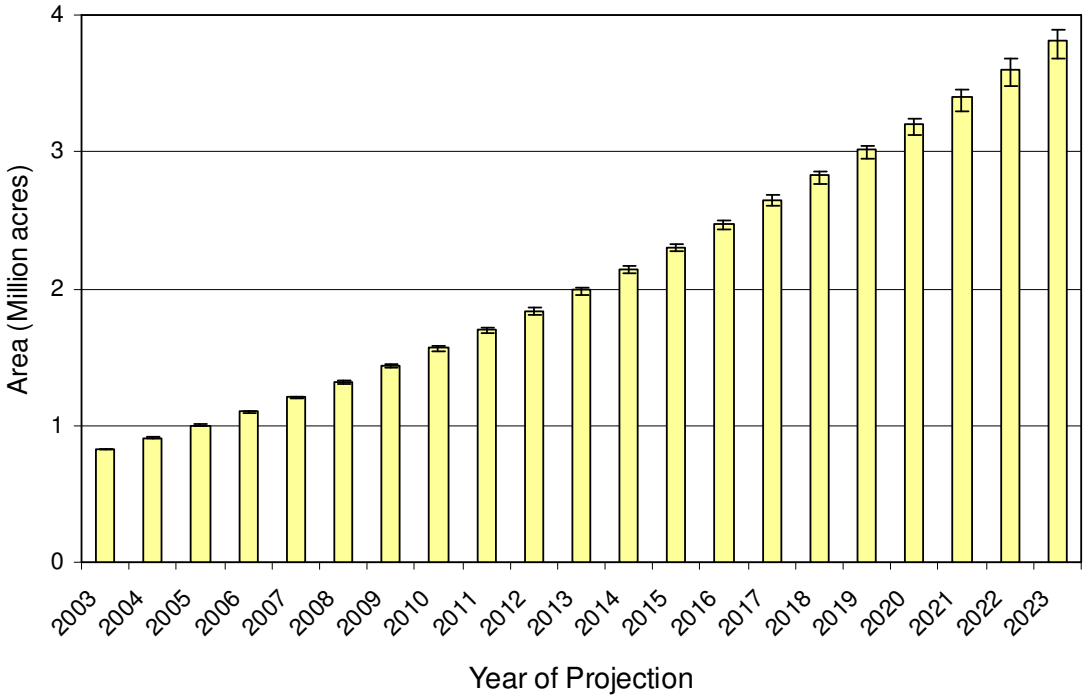


Fig. 15. Projection of the mean (vertical bars represent 95% CI) number of acres invaded by Chinese and European privets in Mississippi and Alabama based on 141 stochastic (Monte-Carlo) simulations.

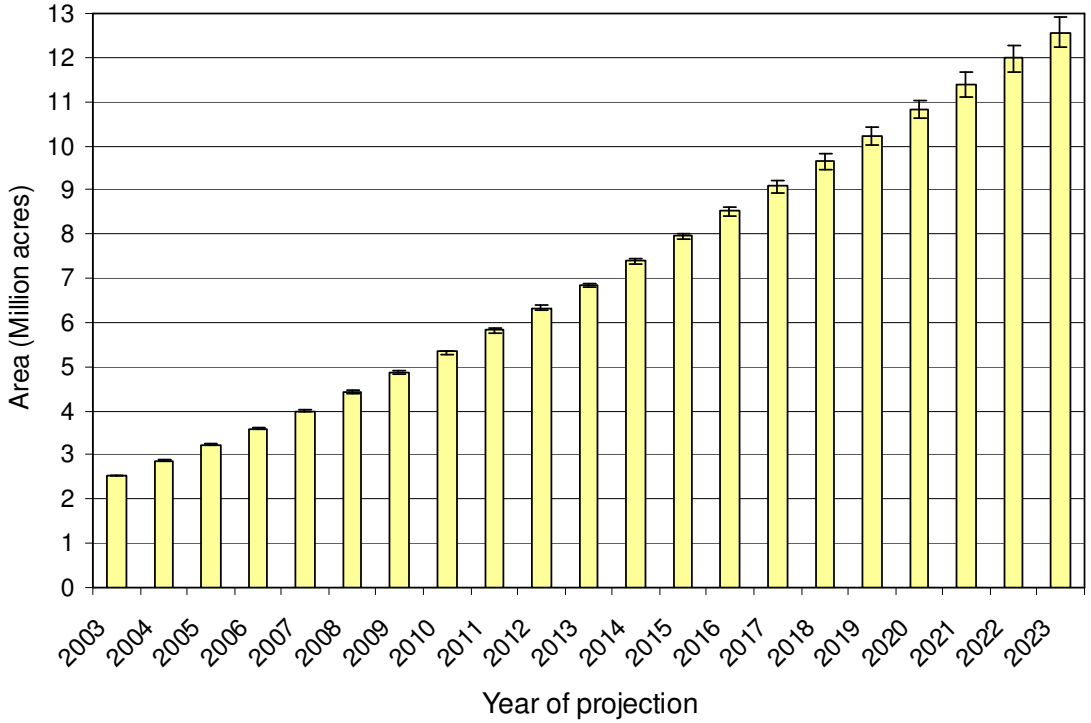


Fig. 16. Projection of the mean (vertical bars represent 95% CI) number of acres invaded by Japanese honeysuckle in Mississippi and Alabama based on 198 stochastic (Monte-Carlo) simulations.

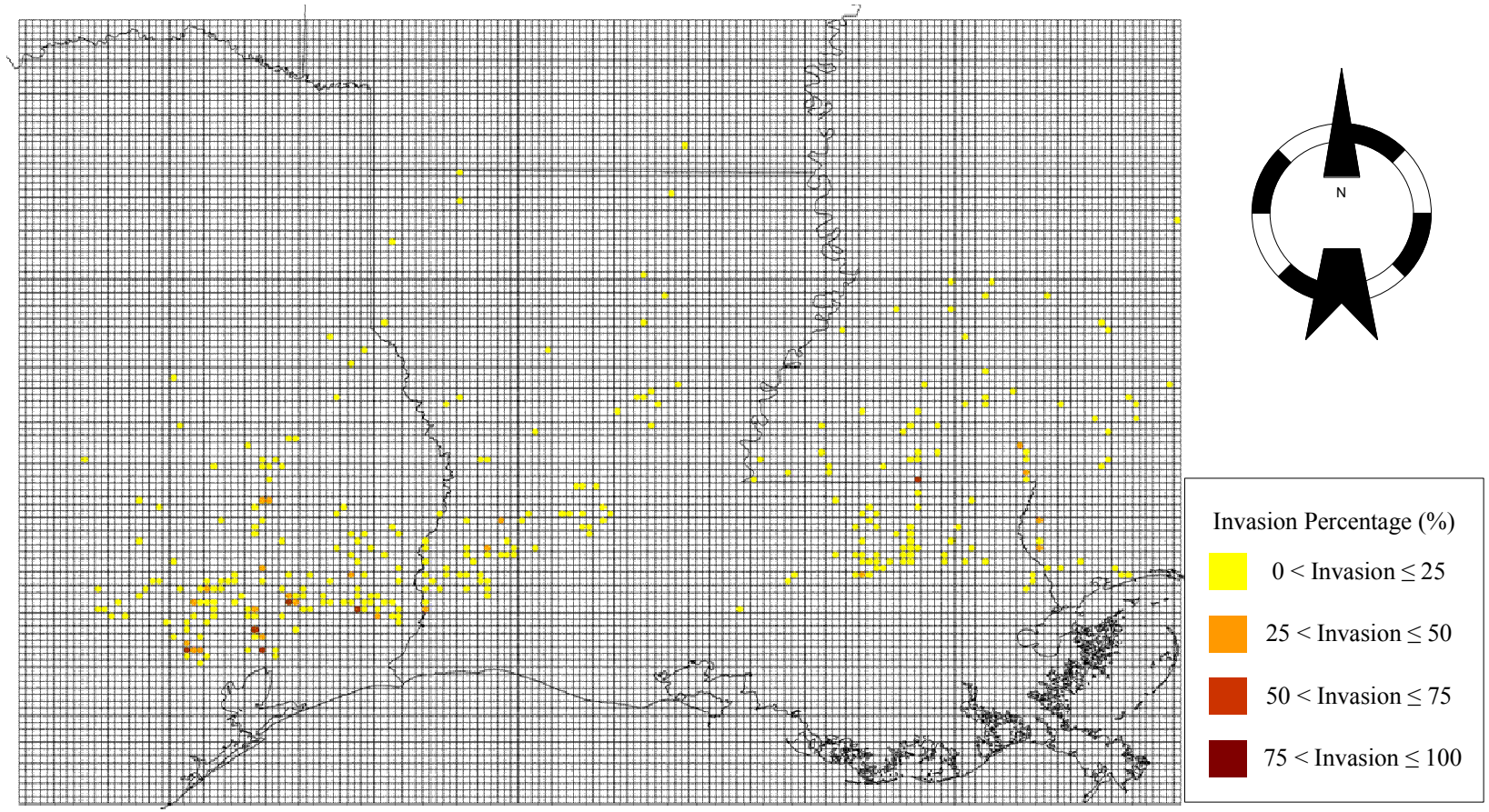


Fig. 17. Observed pattern of Chinese tallow invasion in the year 2003 based on Nonnative invasive plant dataset (USDA, 2008b).

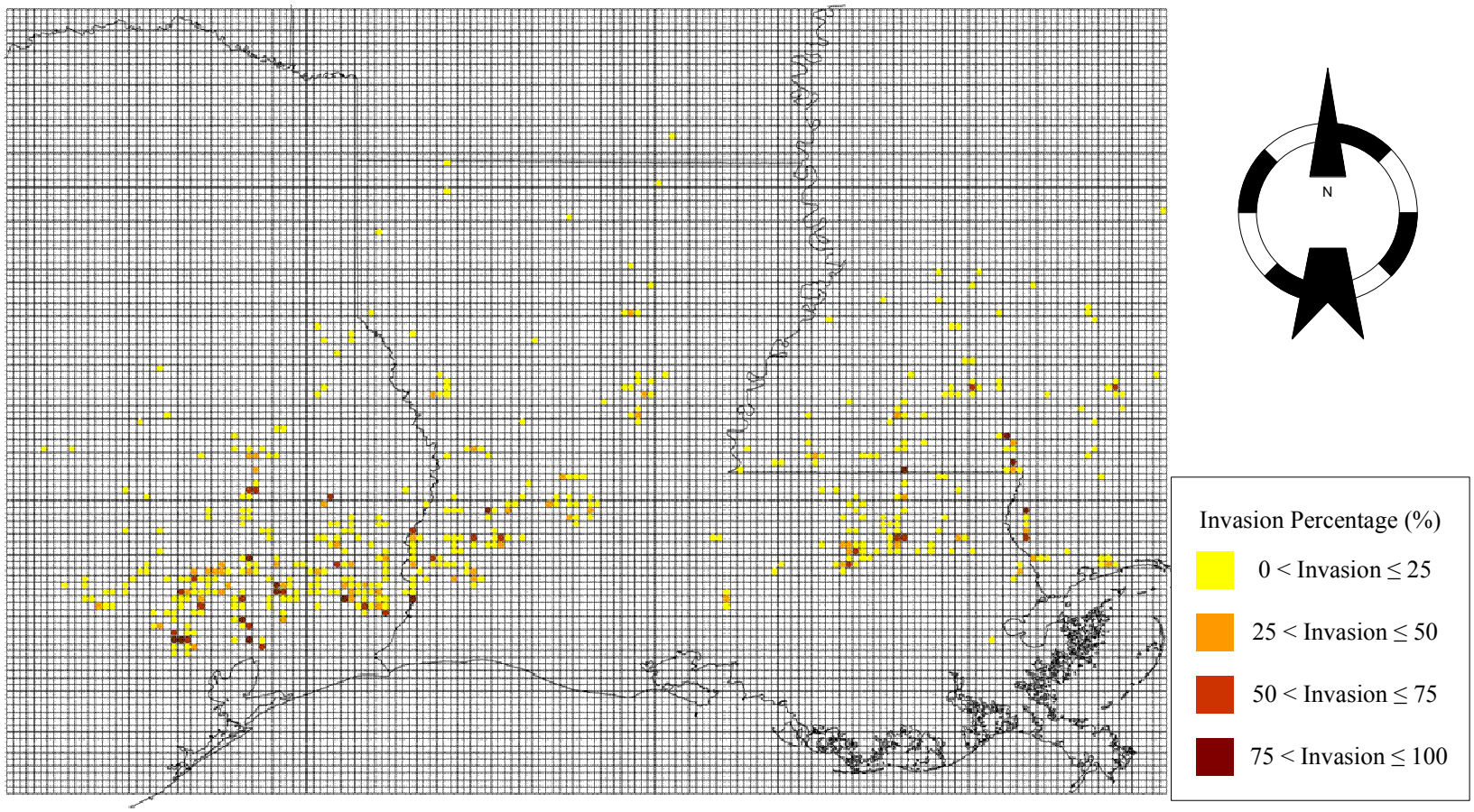


Fig. 18. Simulated pattern of Chinese tallow invasion in the year 2008 based on one randomly-chosen stochastic simulation.

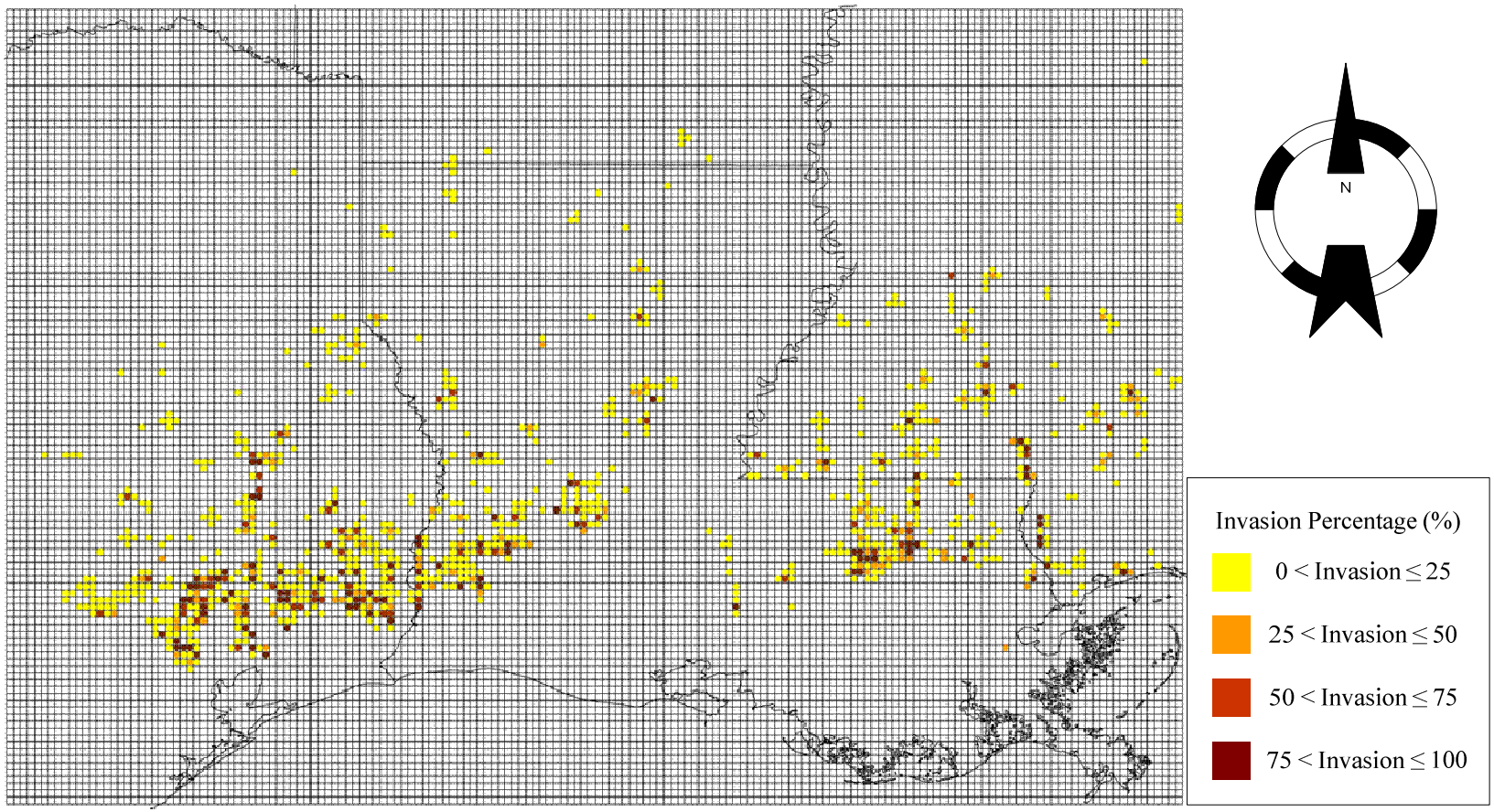


Fig. 19. Simulated pattern of Chinese tallow invasion in the year 2013 based on one randomly-chosen stochastic simulation.

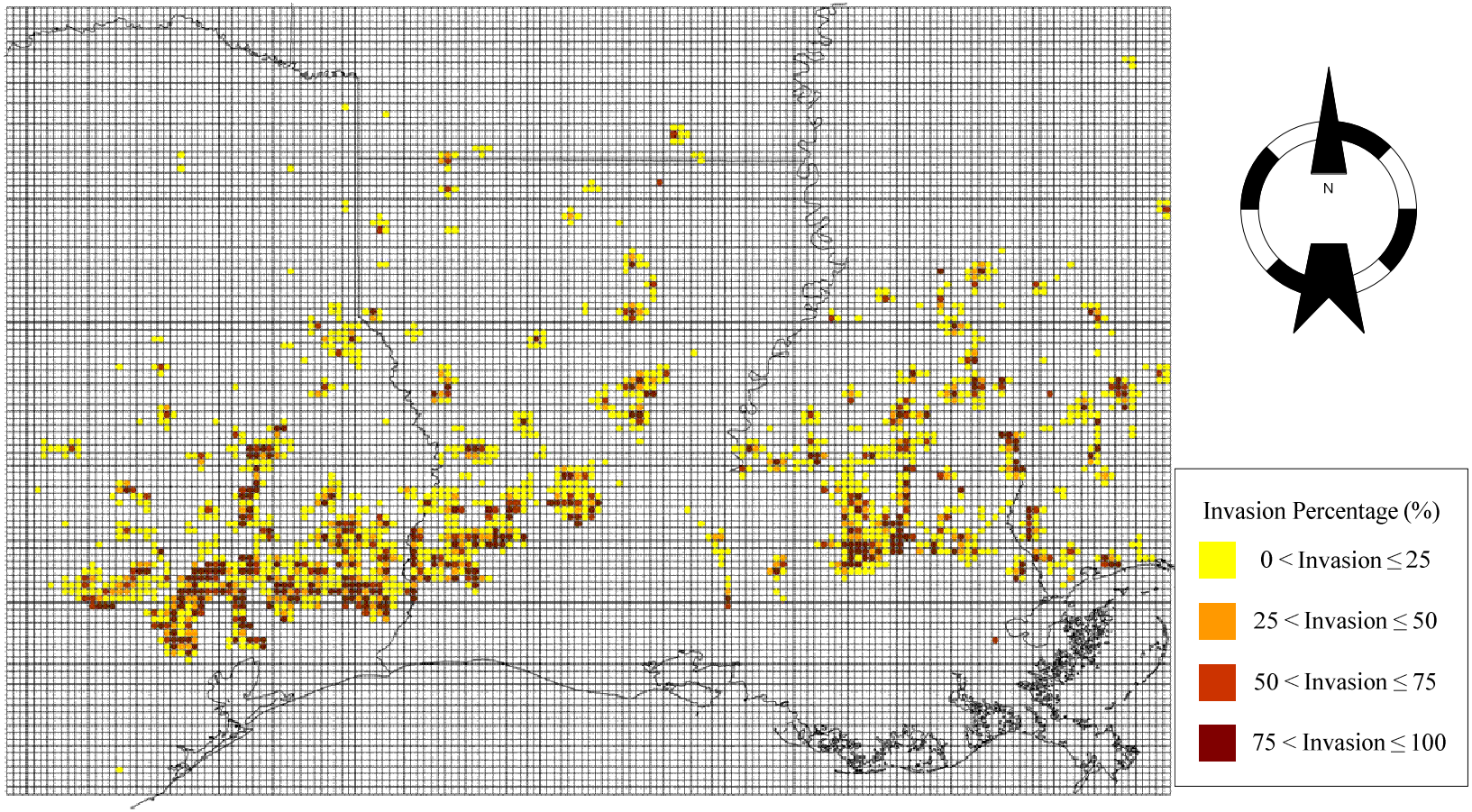


Fig. 20. Simulated pattern of Chinese tallow invasion in the year 2018 based on one randomly-chosen stochastic simulation.

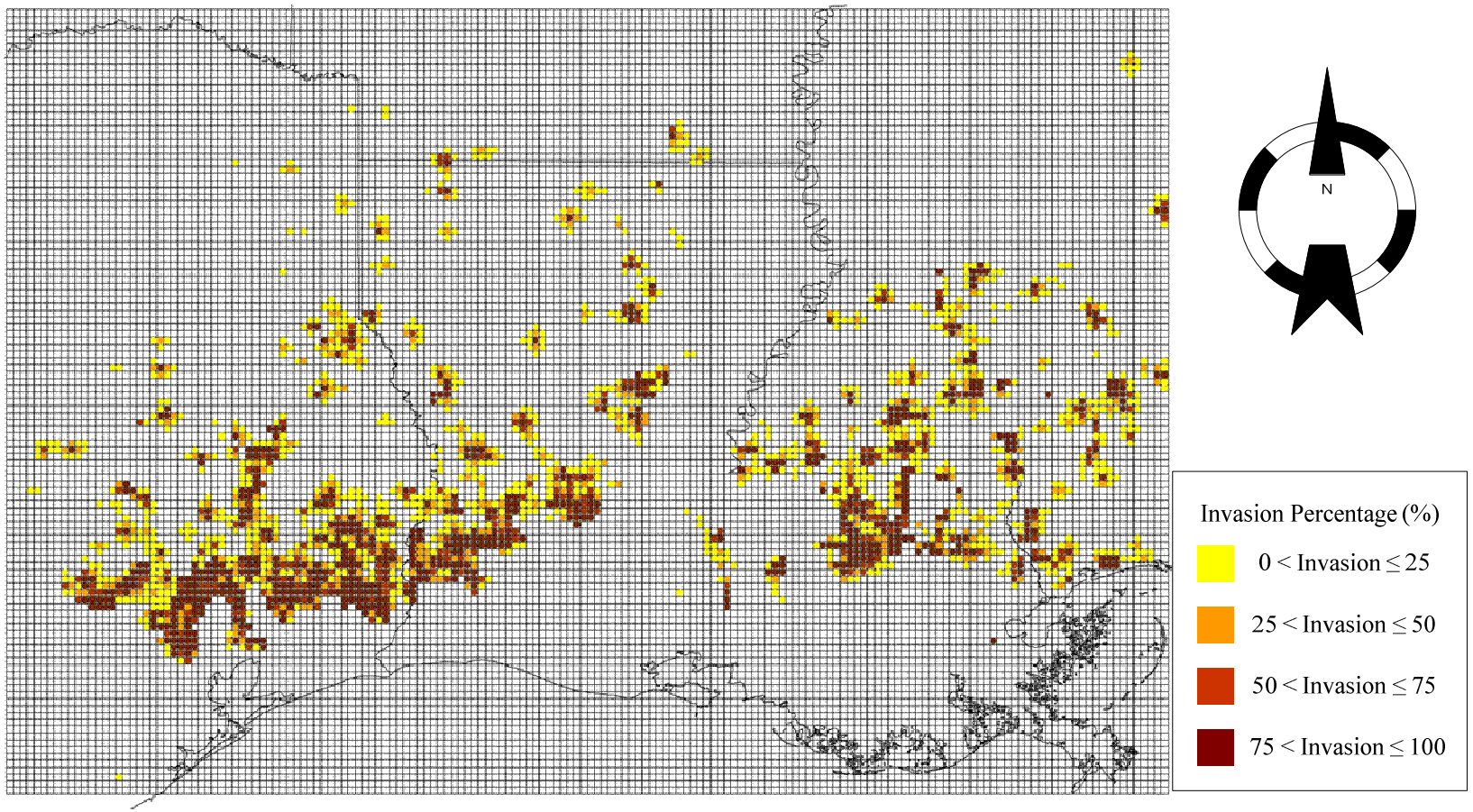


Fig. 21. Simulated pattern of Chinese tallow invasion in the year 2023 based on one randomly-chosen stochastic simulation.

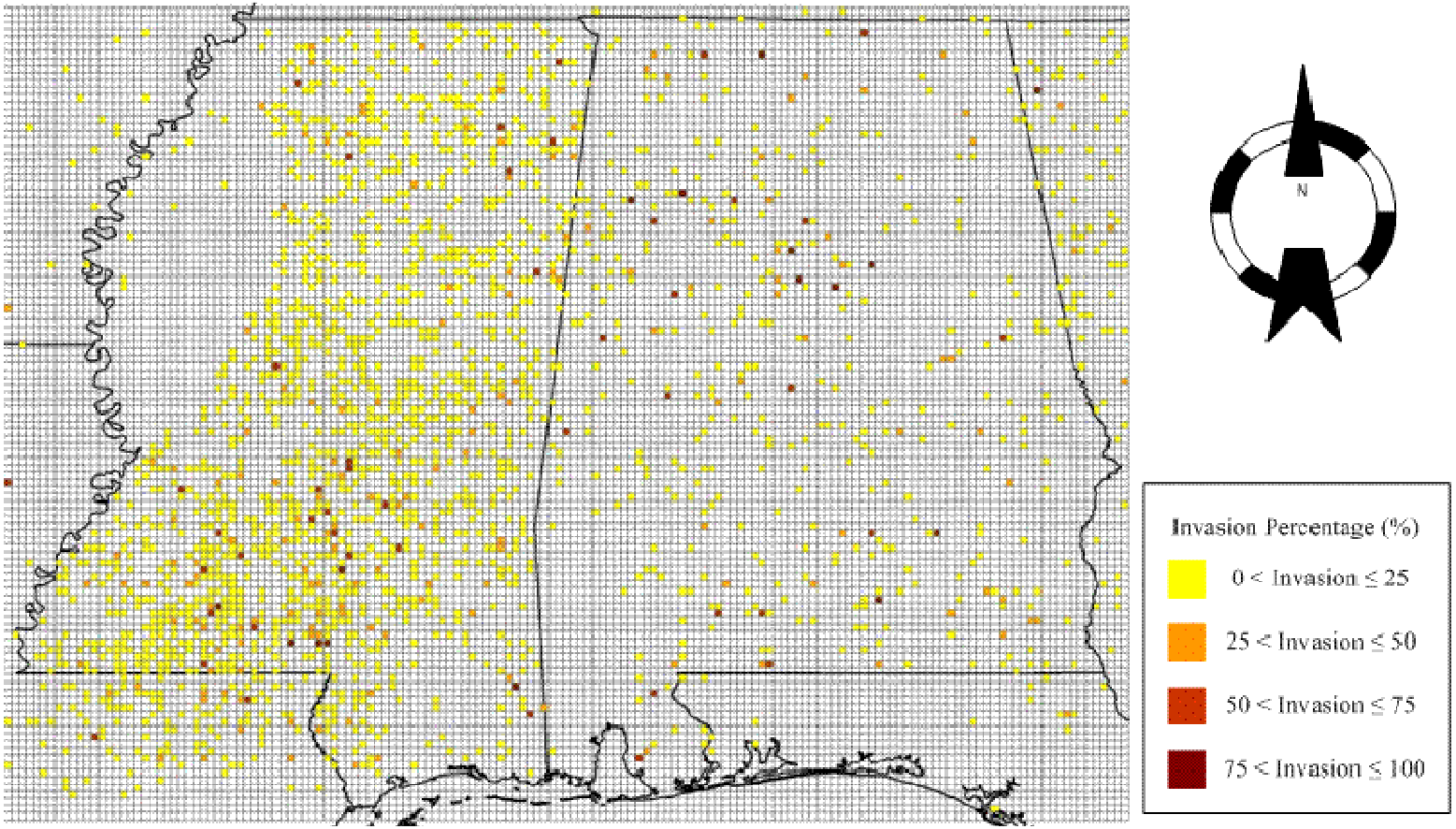


Fig. 22. Observed pattern of Chinese and European privets invasion in the year 2003 based on Nonnative invasive plant dataset (USDA, 2008b).

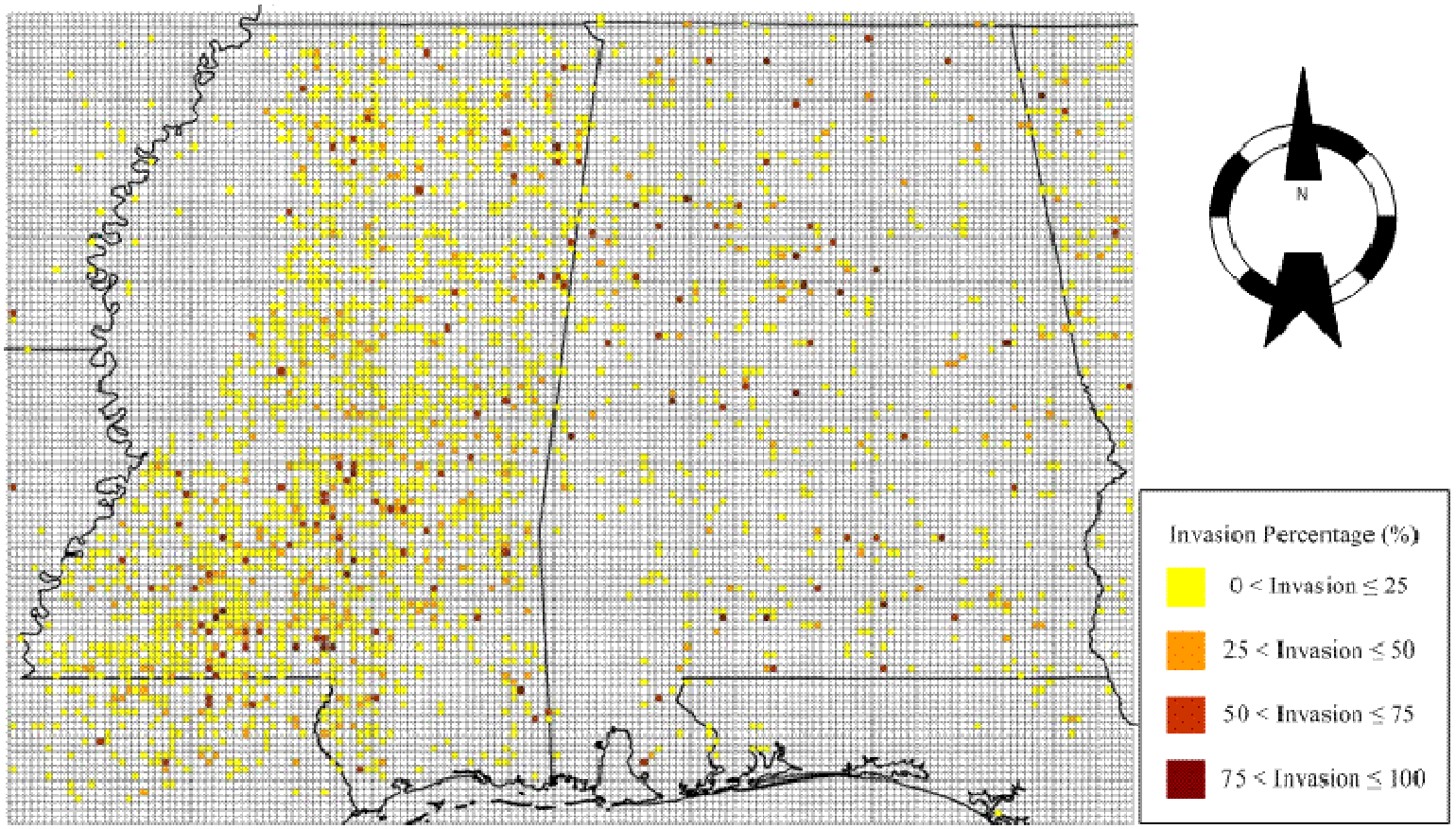


Fig. 23. Simulated pattern of Chinese and European privets invasion in the year 2008 based on one randomly-chosen stochastic simulation.

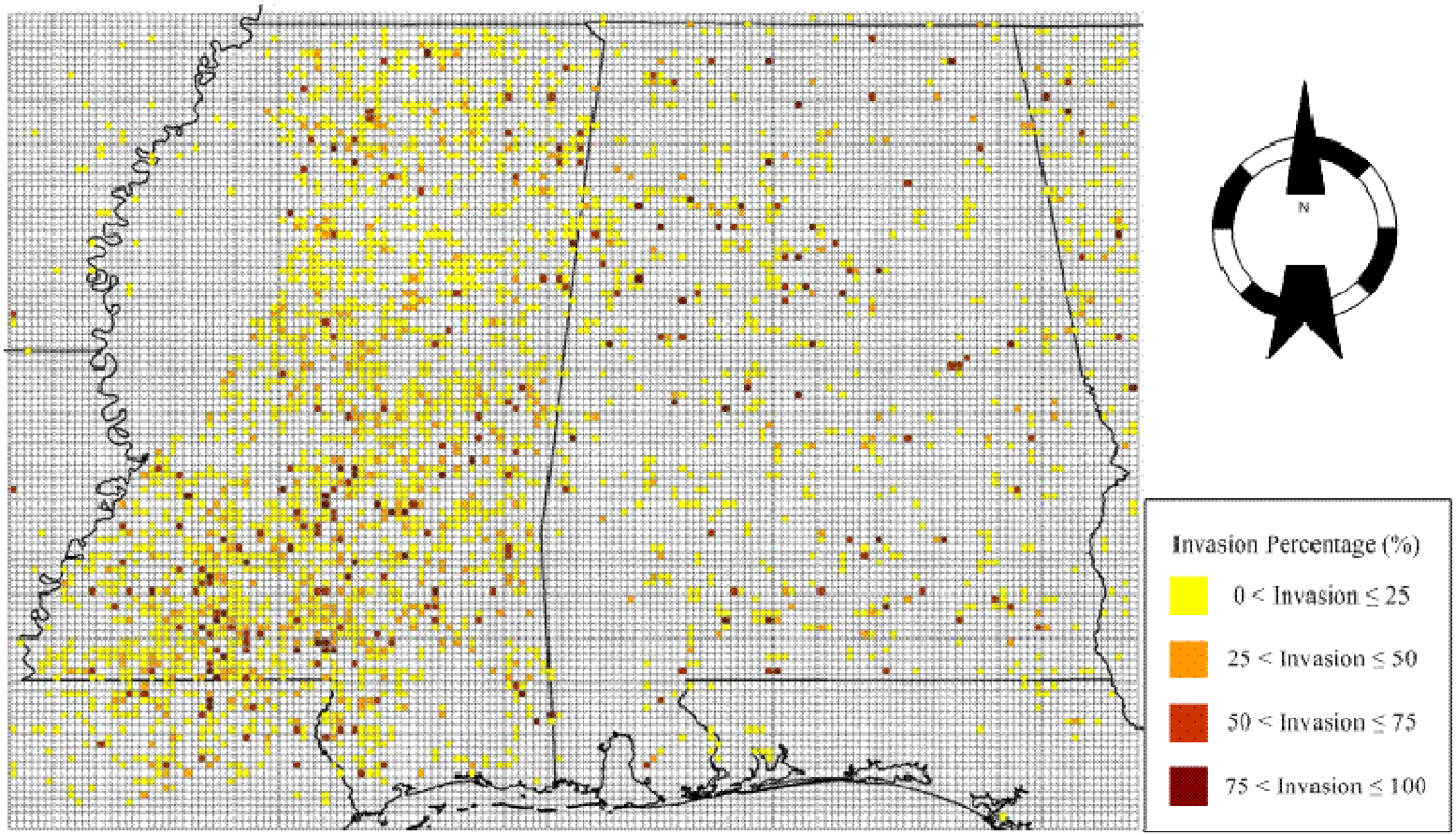


Fig. 24. Simulated pattern of Chinese and European privets invasion in the year 2013 based on one randomly-chosen stochastic simulation.

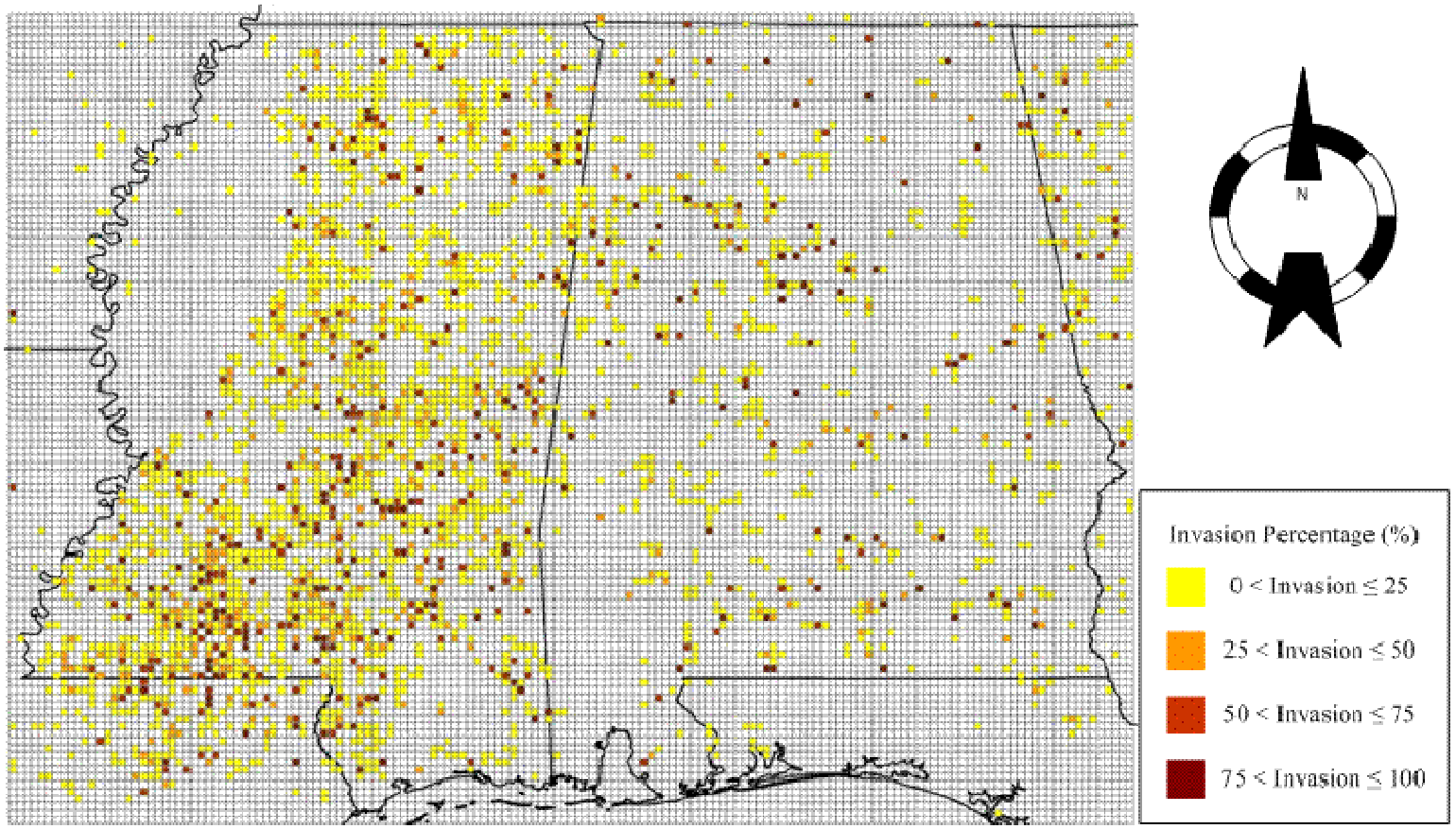


Fig. 25. Simulated pattern of Chinese and European privets invasion in the year 2018 based on one randomly-chosen stochastic simulation.

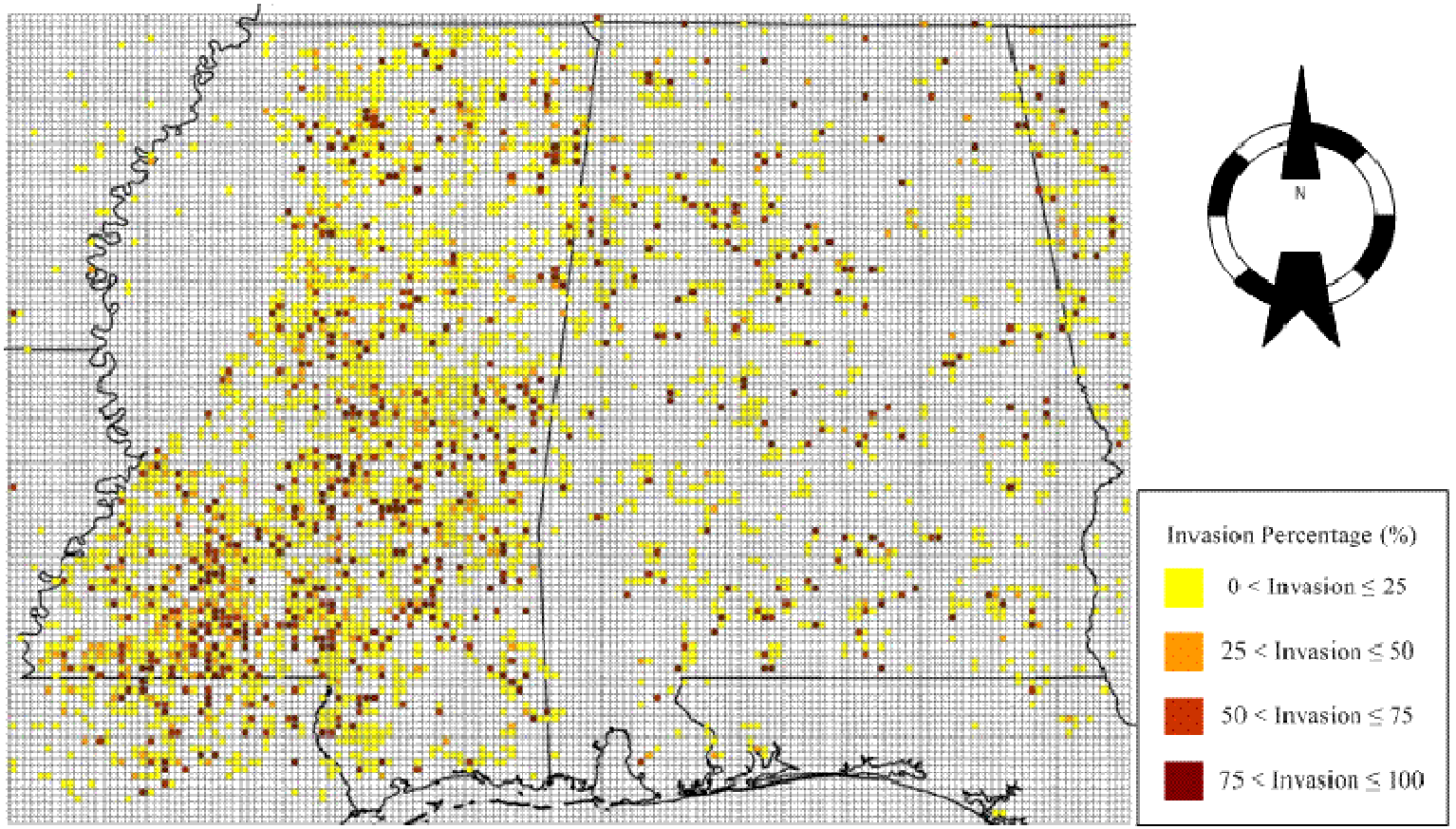


Fig. 26. Simulated pattern of Chinese and European privets invasion in the year 2023 based on one randomly-chosen stochastic simulation.

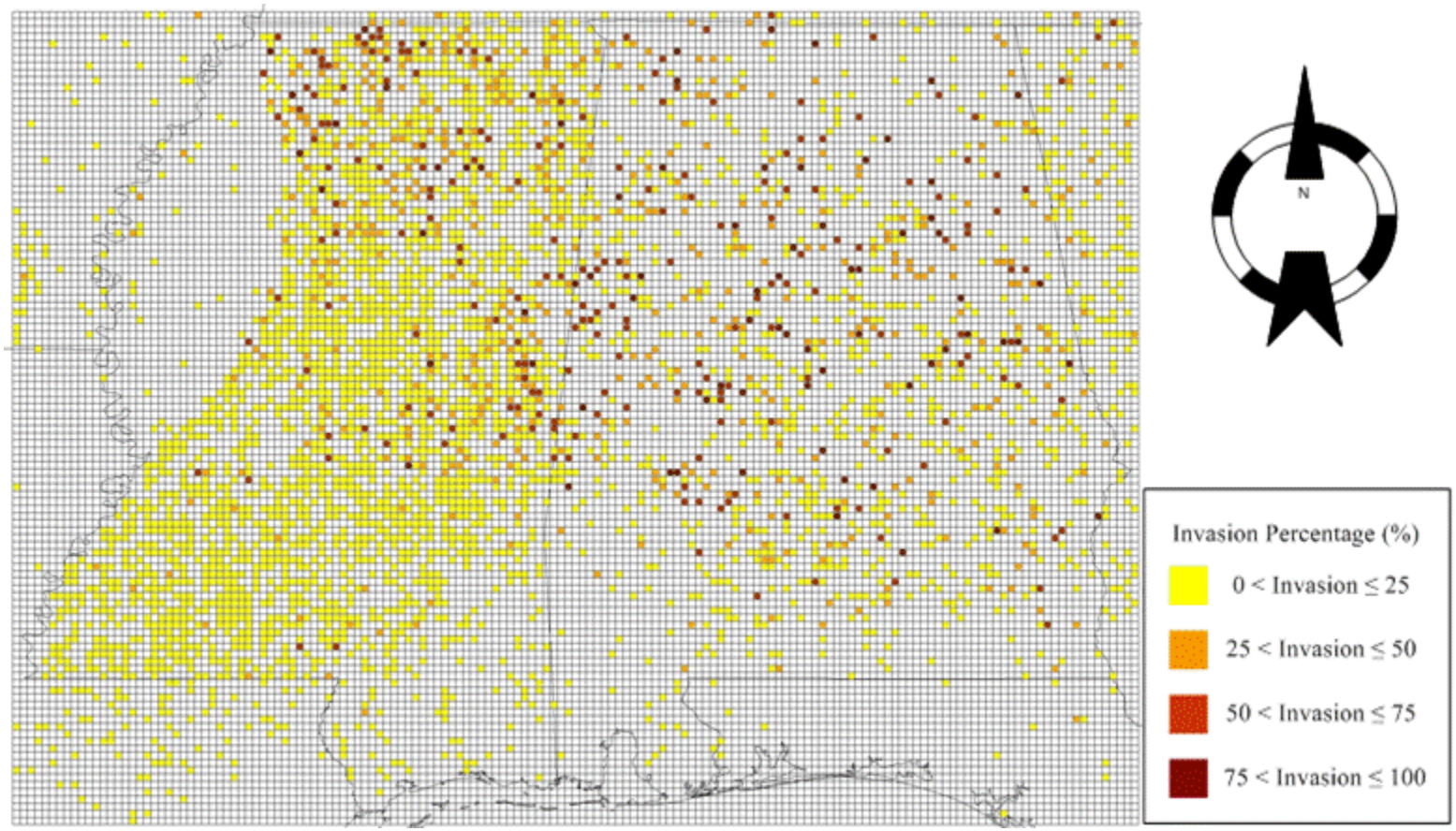


Fig. 27. Observed pattern of Japanese honeysuckle invasion in the year 2003 based on Nonnative invasive plant dataset (USDA, 2008b).

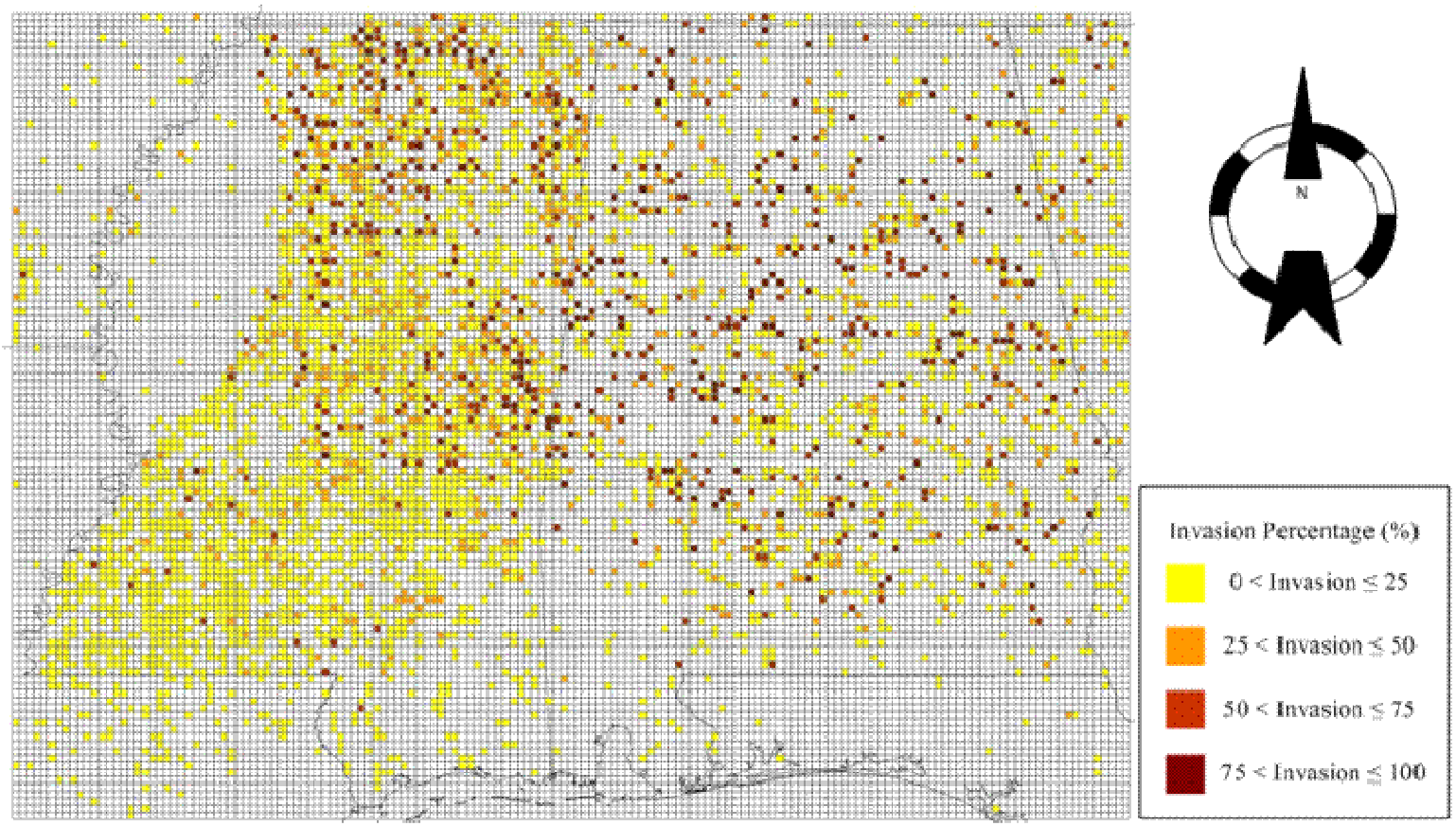


Fig. 28. Simulated pattern of Japanese honeysuckle invasion in the year 2008 based on one randomly-chosen stochastic simulation.

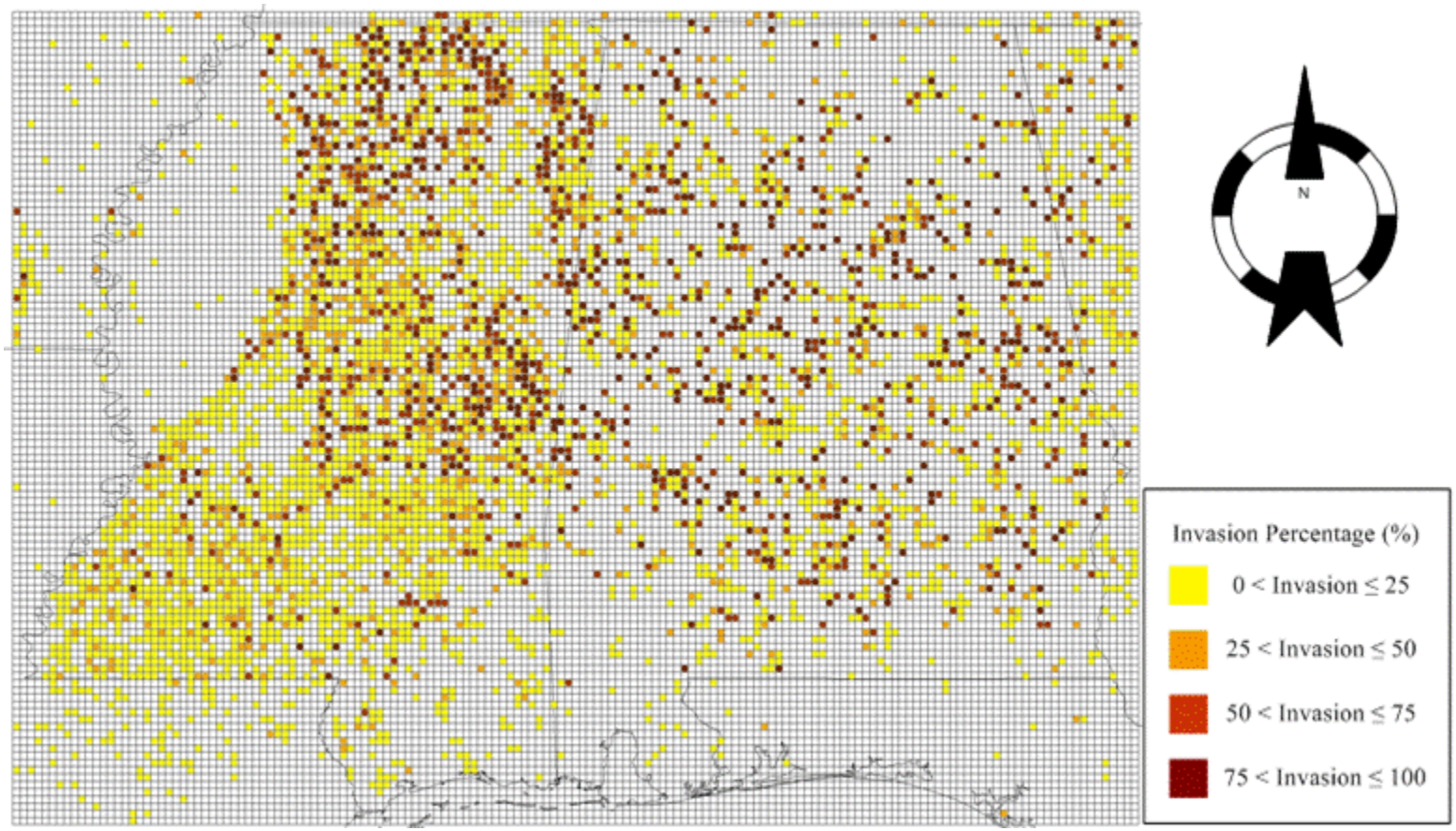


Fig. 29. Simulated pattern of Japanese honeysuckle invasion in the year 2013 based on one randomly-chosen stochastic simulation.

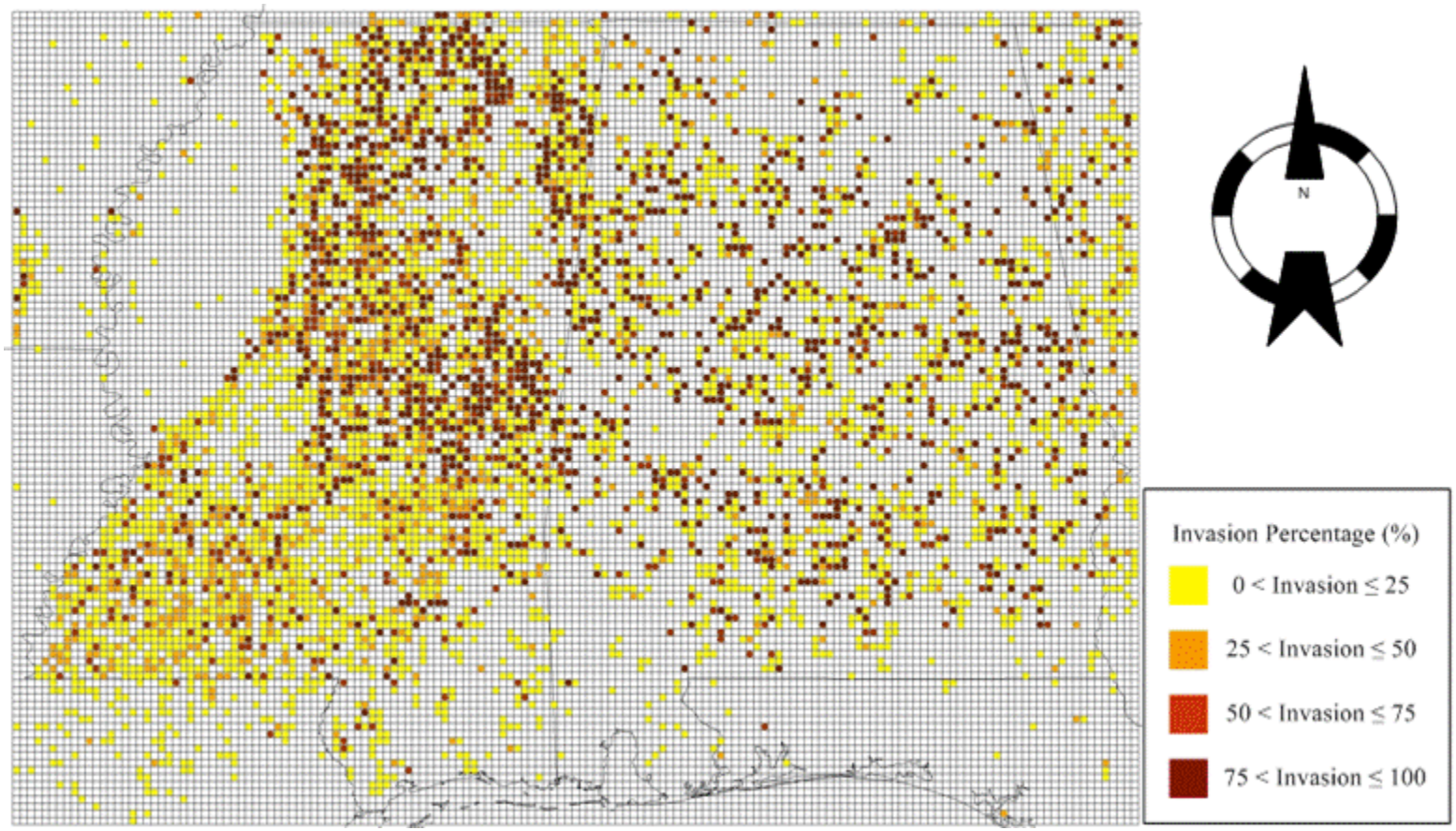


Fig. 30. Simulated pattern of Japanese honeysuckle invasion in the year 2018 based on one randomly-chosen stochastic simulation.

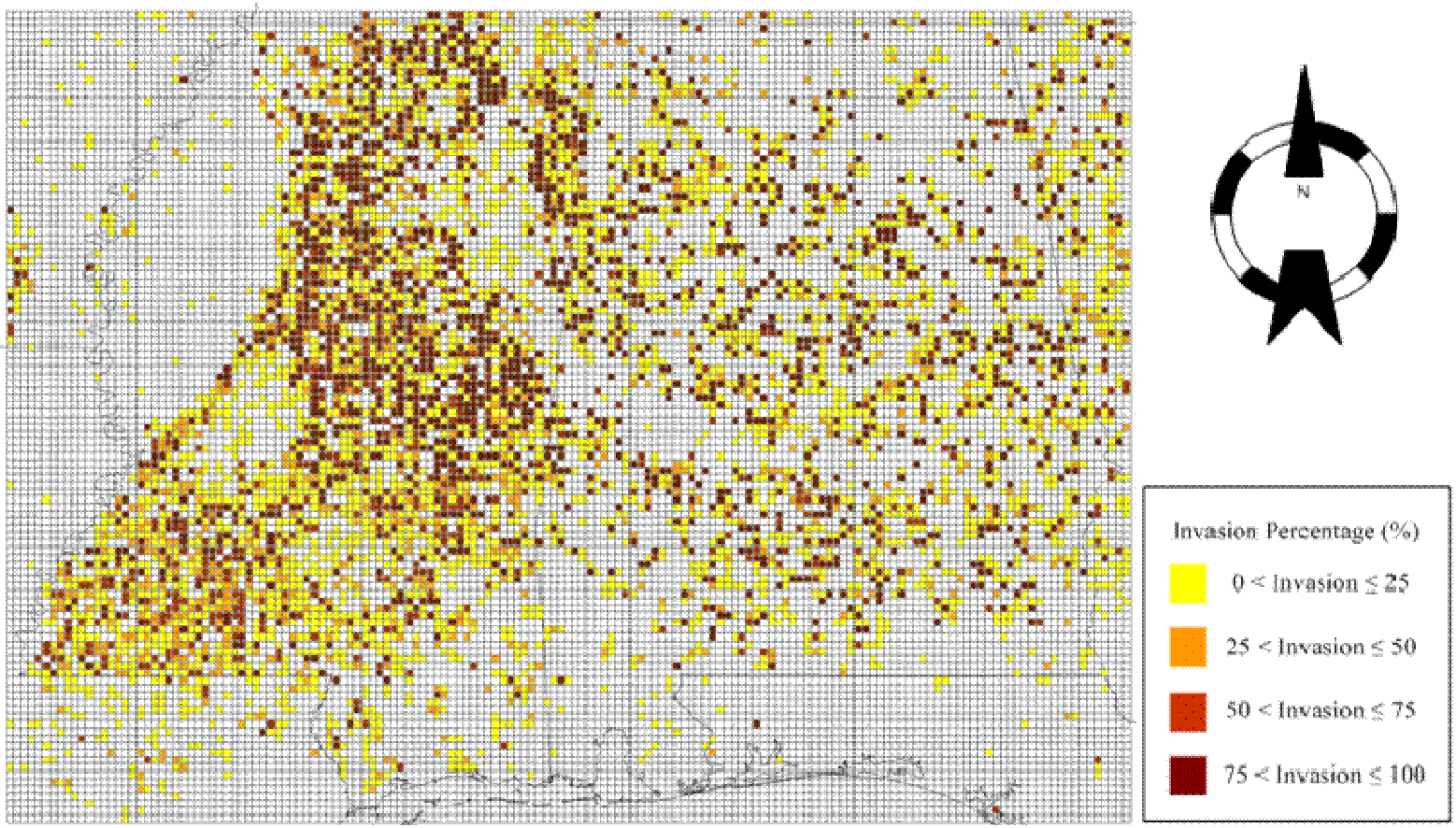


Fig. 31. Simulated pattern of Japanese honeysuckle invasion in the year 2023 based on one randomly-chosen stochastic simulation.

3.4 Discussion

3.4.1 Comparing simulated invasion patterns and velocities of the present study with those reported in previous studies

Both the spatial patterns and the velocities of the simulated invasions are similar to those reported in the literature, but the present study provided not a static but a dynamic prediction with finer resolution (4,927m vs. 55,659m). My model projected the spread of Chinese tallow from the region close to the Gulf of Mexico northward and westward into the forests of Arkansas (Figs. 17-21), at a velocity of approximately 1,000 m/year (985.40 m/year). Pattison and Mack (2008), using their CLIMEX model, which projects species distributions based on key climatic parameters, also projected the northward and westward spread of Chinese tallow through the forests of Arkansas. Renne et al. (2000), based on experiments involving Chinese tallow seed dispersal by birds in coastal South Carolina, estimated a dispersal velocity of around 1,000 m/year.

Although species information on invasion of Chinese and European privets and Japanese honeysuckle was not available, my estimated dispersal velocities of 703.86 and 821.17 m/year were similar to that reported by Morales and Carlo (2006), who used a spatially explicit simulation model to estimate a dispersal velocity of around 800 m/year for plant dispersed by frugivores. Clark *et al.* (2003) used a stochastic model to estimate the following velocities of seed dispersal: 90% of seeds dispersed annually by birds will be dispersed from the parent tree 0-100m, 8% will be dispersed 100-500m, 1.7% will be dispersed 500-5,000m, and 0.3% will be dispersed more than 5,000m.

3.4.2 Possible biases

The present study was restricted to forest land, so it is difficult to see the whole picture, regarding how these invasive species can spread on urban or built-up land, agricultural land, rangeland, water bodies, wetland, and barren land. Thus, result may be biased because: (1) invasive species do not only invade forest land but also other types (Siemann and Rogers, 2003; Zedler Joy and Kercher, 2004; Siemann and Rogers, 2007); and (2) other types of land can serve as a bridge for invasion connecting two or more forest lands (Schierenbeck, 2004; Wilcox and Beck, 2007; Flory and Clay, 2009). In other words, if the present study took all types of land into account, it would make more entries for invasion in forests. Thus, only focusing on how invasion happens on forest land underestimates the invasion problem. However, the present study could only get data from FIA database (USDA, 2008a) which only surveys forest land. Hence, there is a need to survey all types of land. Further, it may be an important topic to figure out how land-use change affects the dispersal of invasive species (Crowl *et al.*, 2008; Jarnevich and Stohlgren, 2009).

Pattison and Mack's (2008) study indicated that the spread of Chinese tallow could occur along rivers and other sources of perennial water in Texas and Oklahoma. This situation can create long distance dispersal. The present study assumed the spread is like diffusion, so it may occur by wind or animals, which only took into account short distance dispersal and ignored long distance dispersal. Hence, there is a need to better understand how to estimate long distance dispersal, such as the dispersal ability for carrying seeds by hydrologic system. Also, it would be very interesting to discover how

human activities and population affect the invasion process. These are also important components for long distance dispersal. There are a few references that already show that human transportation facilitates the spread of invasive species, and that invasion increments follow human population growth (Davis *et al.*, 2000; Crowl *et al.*, 2008; Flory and Clay, 2009).

FIA field crews measure permanent ground plots, which have a spatial sampling intensity of approximately one plot per 6,000 acres. In this study, I represented the population in 6,000 acres by using the information of one plot and following the advice by Bechtold and Patterson (2005). This approach has the advantage of simplicity, but has the potential to incur bias if the nonsampled area is not representative of the rest of the population. Many methods of accounting for nonsampled areas are under investigation by FIA, including remote sensing both for direct measurement of a subset of attributes and for use in identidying similar plots for imputation purpose (Bechtold and Patterson, 2005). Hence, this model could be improved in the near future.

The present study used habitat quality to predict growth rate, which was a novel idea that used limited information to generate growth rate in each habitat cell, thus avoiding the assumption of landscape homogeneity (Hastings, 1990, 1996; Hastings *et al.*, 2005; Jarnevich and Stohlgren, 2009). Also, this approach could be a powerful tool to predict how climate change affects invasion by changing climatic variables, while holding other variables constant, to derive new logistic regressions, new habitat quality indexes, and new associated growth rates (Crowl *et al.*, 2008). Because the present study only had data collected within a 5-year period, it seemed more reasonable to keep

the habitat quality index in each cell constant. However, this is a risky assumption because there is always something changing in the environment. Hence, there is a need to have continuous, long-term survey, so it can improve the simulation model by updating the logistic regression, estimated habitat quality, and associated growth rate.

3.4.3 Possible long-term invasion trends

I assumed that population growth is logistic growth. However, the simulated land cover changes for these invasive species over the next 20 years indicated that all these invasions still were in the exponential growth phase (Figs. 14-16). Chinese tallow had invaded only 12.84% of forest land (51.77 million acres) in East Texas and Louisiana, and Chinese and European privets and Japanese honeysuckle had invaded only 5.65% and 18.61%, of forest land (67.45 million acres) in Mississippi and Alabama. Using the simulated data from Figures 14-16, I estimated the parameters of the integral from the logistic growth equation and used them to estimate how much time these three species would need to complete colonizing all forest land within the study area if there is no invasion control:

$$\because N_t = \frac{K}{1+\exp(a-rt)} \text{ and let } K = 100$$

$$\Rightarrow [1] \quad N_0 = \frac{100}{1+\exp(a)} \quad \text{and} \quad [2] \quad N_{20} = \frac{100}{1+\exp(a-20r)}$$

$$From \quad [1] \quad N_0\left[1+\exp(a)\right] = 100$$

$$\Rightarrow \quad [3] \quad a = \ln\left(\frac{100}{N_0} - 1\right)$$

$$From \quad [2] \quad N_{20}\left[1+\exp(a-20r)\right]=100$$

$$\Rightarrow \quad [4] \quad r=\frac{1}{20}\left[a-\ln\left(\frac{100}{N_{20}}-1\right)\right]$$

$$Apply \quad [3] \quad to \quad [4] \quad \Rightarrow r=\frac{1}{20}\left[\ln\left(\frac{100}{N_0}-1\right)-\ln\left(\frac{100}{N_{20}}-1\right)\right]$$

Hence, I calculated $a_t = 5.85$ and $r_t = 0.20$ for Chinese tallow, $a_p = 4.39$ and $r_p = 0.08$ for Chinese and European privets, and $a_h = 3.24$ and $r_h = 0.09$ for Japanese honeysuckle. I then projected long-term, logistic growth for each species and estimated that Chinese tallow would be observed in forests in East Texas and Louisiana in 75 years, Chinese and European privets would be observed in forests in Mississippi and Alabama in 150 years, and Japanese honeysuckle would be observed in forests in Mississippi and Alabama in 120 years (Figs. 32, 33, and 34). Hence, if there were no invasion control, these invasive species eventually would be observed in all forests.

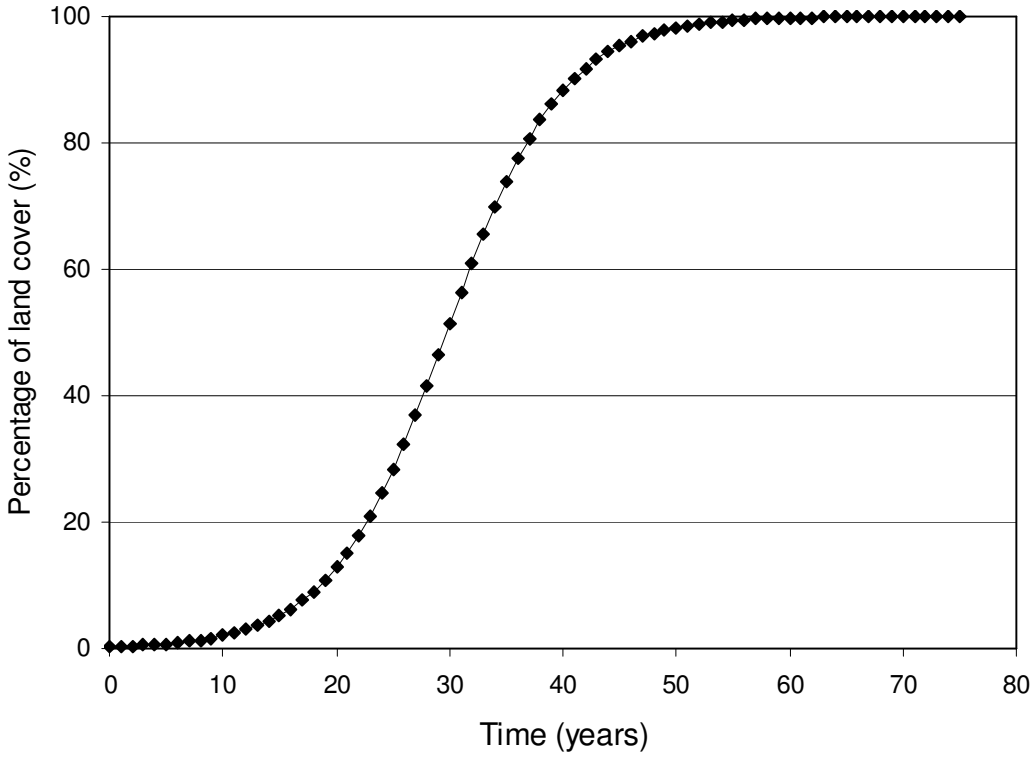


Fig. 32. Possible long-term invasion trends for Chinese tallow in East Texas and Louisiana projected by the logistic growth model.

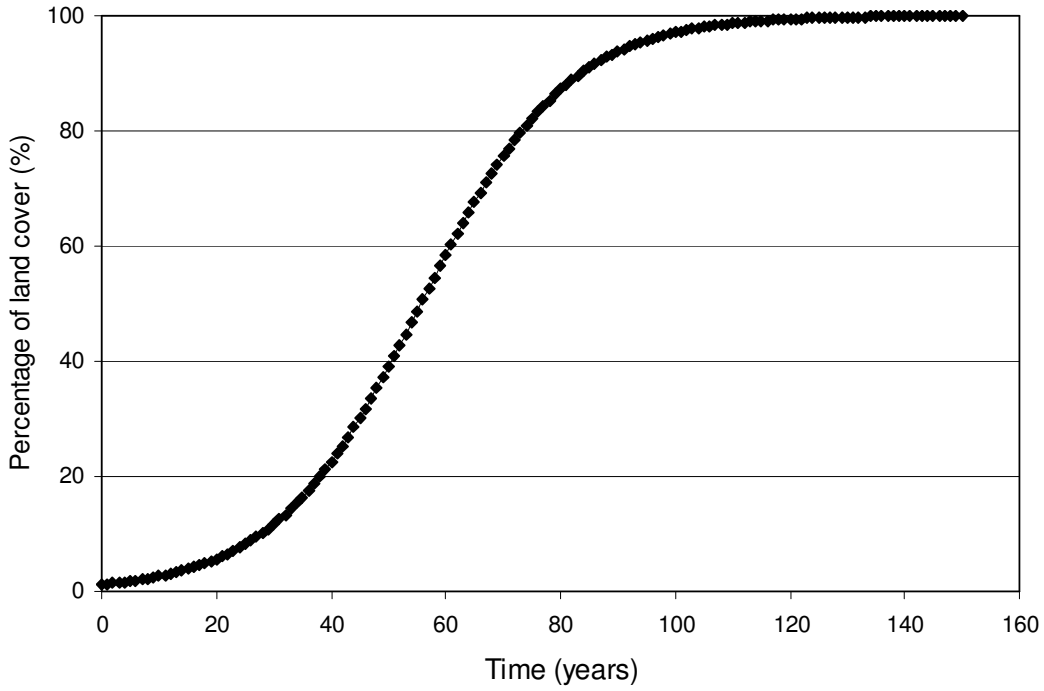


Fig. 33. Possible long-term invasion trends for Chinese and European privets in Mississippi and Alabama projected by the logistic growth model.

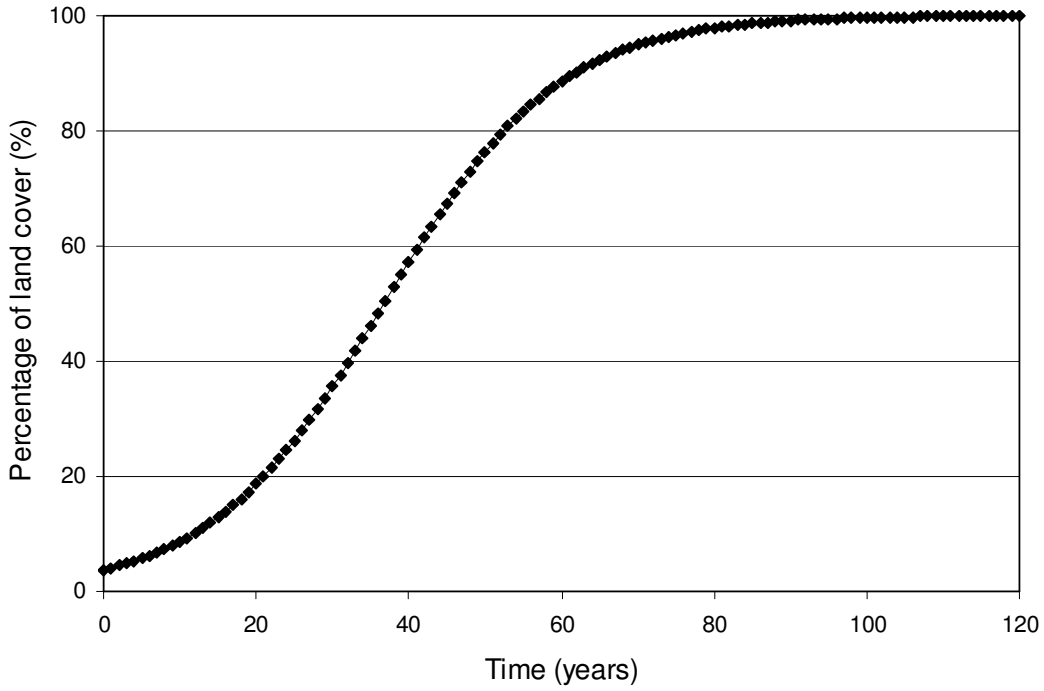


Fig. 34. Possible long-term invasion trends for Japanese honeysuckle in Mississippi and Alabama projected by the logistic growth model.

3.4.4 Coexistence

An ecosystem is a complex environment and coexistence and interactions among multispecies are the norm. In statistics, multicategory logit models can be applied to modeling categorical responses with more than two categories (Agresti, 2007). In quantitative ecology, Lotka-Volterra model can be applied to model multispecies population dynamics with dispersal (Okubo and Levin, 2001). The present study did not consider coexistence for Chinese and European privets and Japanese honeysuckle even though I ran the simulations for these two invasive plant species in the same study area. This is because I have checked if it is appropriate to add one species as a variable into another species' model. I added one more variable which was if there were Chinese and European privets (0 or 1) in Japanese privet logistic regression model. The result shows that elevation, wing damage, and land ownership are excluded in the model, but Chinese and European privets are included and have a significantly positive effect for Japanese honeysuckle invasions (Table 8). However, I can reject the null hypothesis on its goodness of fit because the *p*-value of Hosmer-Lemeshow test is less than 0.0001. Also, the model with Chinese and European privets contains fewer variables but high deviance (Deviance=22895.66), which means this model is not appropriately estimated. Coexistence is very complex and beyond the scope of this study. However, there is no doubt that it is important to discover how two or more invasive species coexist or interact with each other.

Table 8. Logistic regression results for Japanese honeysuckle invasions estimated with and without Chinese and European privets in the southern U.S.

Variable	Model fit for Japanese honeysuckle without Chinese and European privets			Model fit for Japanese honeysuckle with Chinese and European privets		
	Estimated coefficient	Odds ratio	P-value	Estimated coefficient	Odds ratio	P-value
Elevation	-0.0001	0.9999	0.0359	—	—	—
Slope	-0.0253	0.9750	<0.0001	-0.0219	0.9783	<0.0001
Proximity to water bodies	0.2080	1.2312	<0.0001	0.1604	1.1740	<0.0001
Stand age	-0.0147	0.9854	<0.0001	-0.0144	0.9857	<0.0001
Site productivity	0.2676	1.3068	<0.0001	0.2435	1.2757	<0.0001
Plant species diversity	0.3580	1.4305	<0.0001	0.3340	1.3965	<0.0001
Timber harvest	0.1631	1.1772	<0.0001	0.1589	1.1722	<0.0001
Site preparation	-0.6060	0.5455	<0.0001	-0.5511	0.5763	<0.0001
Distance to the nearest road	-0.0781	0.9249	<0.0001	-0.0653	0.9368	<0.0001
Fire damage	-0.4229	0.6551	0.0387	-0.3494	0.7051	0.0387
Animal damage	0.3991	1.4905	<0.0001	0.2382	1.2690	<0.0001
Wind damage	0.2435	1.2757	<0.0001	—	—	—
Land ownership	0.8025	2.2311	<0.0001	—	—	—
Chinese and European privets	—	—	—	0.1968	1.2175	<0.0001
Constant	-2.8363	0.0586	<0.0001	-2.5040	0.0818	<0.0001
P-value of Hosmer-Lemeshow test		0.1900			<0.0001	
Log-likelihood ratio		11,419.04			11,447.83	
AIC		22,866.08			22,919.66	
Overall correct prediction		61.0%			54.7%	
Number of observations		34,671			34,671	

3.5 Conclusions

This study developed a dispersal model which includes a logistic growth model and a diffusion model and applied it to estimate invasions by Chinese tallow in East Texas and Louisiana and by Chinese and European privets and Japanese honeysuckle in Mississippi and Alabama during the next 20 years.

In the logistic growth model, the present study tried to link the growth rate and the habitat quality index, so it could overcome the data limitation that most forest cells did not contain 2-cycle surveys, and estimate the appropriate growth rate for each cell. In the diffusion model, the present study used Mantel's test as a criterion to derive dispersal velocities of 985.40, 703.86, and 821.17m/year for Chinese tallow, Chinese and European privets, and Japanese honeysuckle, respectively.

Twenty-year projections of invasions by Chinese tallow, Chinese and European privets, and Japanese honeysuckle indicated that these invasive species will colonize approximately 6.65 million acres (12.84% of forest lands) in East Texas and Louisiana, 3.81 million acres (5.65% of forest lands) in Mississippi and Alabama, and 12.55 million acres (18.61% of forest lands) in Mississippi and Alabama, respectively. The growth curves for all these invasive species are still exponential over the next 20 years (Figs. 14, 15, and 16), and, if there is no harvest or control, these invasive species eventually would be observed in all forests in these four states (Figs. 32, 33, and 34).

The merit of this study is that it integrates statistical forecasting approaches with analytical models to project ecological invasions in time and space. Furthermore, the models can be updated with the latest FIA data, and the approach can be applied to other

invasive species or locations. Spatially-explicit simulation environments show great promise for effectively integrating statistical and analytical approaches to predict the spread of invasive species, thus drawing on the strengths and avoiding some of the shortcomings associated with each approach individually and data limitations. The results on occupation and spread also provide potential for combining the information from timber markets and invasion control companies to estimate possible economic losses under different control scenarios. Based on these findings, optimal mitigation strategies can be developed.

4. COSTS OF CONTROLLING CHINESE TALLOW (*Triadica sebifera* (L.) Small), CHINESE AND EUROPEAN PRIVETS (*Ligustrum sinense* Lour. and *Ligustrum vulgare* L.), AND JAPANESE HONEYSUCKLE (*Lonicera japonica* Thunb.) ON SOUTHERN U.S. FORESTLANDS

4.1 Introduction

Invasive species have profoundly negative impacts on natural environments at both local and global levels. The impacts of invasive species are immense, insidious, and usually irreversible (McNeely *et al.*, 2001). For example, invasive species cause over $120 billion per year of damage to agriculture and 400 of the 958 species that are listed as threatened or endangered under the Endangered Species Act are considered to be at risk primarily because of competition with and predation by invasive species in the United States (Pimentel *et al.*, 2005; Crowl *et al.*, 2008). However, several studies have shown that not only the number of invasive species but also their abundances keep increasing because of increasing trade and travel and climate change (Simberloff, 2000; McAusland and Costello, 2004; Katharina *et al.*, 2007).

There is great potential for Chinese tallow, Chinese and European privets, and Japanese honeysuckle to expand their ranges (see previous two sections). Hence, there is a need to estimate the economic losses associated with invasive alien plant species and to provide the best control strategy. Yet, estimating the full spectrum of economic impacts that are associated with invasive alien plant species now or in the future is difficult because of the poor information available and the uncertainty involved. The

first challenge is to trace where and how fast an invasive alien plant species spreads (Merriam and Feil, 2002). Second, an invasive alien plant species causes different types and levels of damages, such as timber losses (Smith and Darr, 2004), disruption of native ecosystems (Siemann and Rogers, 2007), and loss of biodiversity of native species (Merriam and Feil, 2002). The occupation models and dispersal models for invasive species developed in the previous two sections are good starting points for estimating timber losses and making mitigating decision. Hence, the objectives of this section are (a) to assess economic losses in forest productivity under different control or management scenarios (Smith and Darr, 2004; Rudis *et al.*, 2006) by incorporating an economic component into the simulation model described in the previous section and (b) to develop the best control strategy for each of the invasive plant species based on the economic assessment.

4.2 Methods

I used the occupation and dispersal models for Chinese tallow, Chinese and European privets, and Japanese honeysuckle to project future invasions. The data used for the economic analysis were drawn from the Forest Service (Bentley *et al.*, 2005; Johnson *et al.*, 2007; Bentley *et al.*, 2008; Johnson *et al.*, 2008a, b; Xu, 2008; Howell and Johnson, 2009; Johnson *et al.*, 2009a; Mathison and Schnabel, 2009; Schiller and Hendricks, 2009), TPO (Timer Product Output) (USDA, 2007b), Timber Mart-South data (timber industry) (TMS, 2009), and interviews of several invasive plant control companies.

I projected the economic impacts in forest productivity for different control levels including no control. Some studies have shown that eradication is viable at the early stage of invasion (McNeely *et al.*, 2001; Olson and Roy, 2002; Liebhold and Bascompte, 2003; Koike *et al.*, 2007). This implies that early detection is important in mitigating and controlling invasions. Hence, there is a need to provide estimates of temporal trends in economic losses in forest productivity. Such information is of interest to policy makers and land owners.

4.2.1 Framework for estimating economic impacts

In general, expected costs in forest productivity, $E(C)$, depend on the size of the invasion (damage costs in timber losses), the effort to reduce the size of the invasion (control costs), and the searching effort (searching costs) (Olson and Roy, 2002; Mehta *et al.*, 2007).

For damage costs, the size of land area where invasive plant species invade is directly related to the amount of timber losses, because their major effect is forest stand replacement with little impediment of growth of commercial timber species (Cain, 1992; Bruce *et al.*, 1995; Hamann, 2001; Merriam and Feil, 2002; Stinson *et al.*, 2006). Hence, I defined the damage cost caused by the invasion as:

$$D(x_i) = x_i \times V_i \times P_i$$

where $D(x_i)$ is the value of timber losses in cell i, x_i is size of the invaded area (ha) in cell i, V_i is the original timber productivity without invasion (m^3/ha) in cell i, and P_i is the market price of timber ($/$m^3$) in cell i.

Control costs vary with the size of invasion and invasive species. Here, I denote control costs ($) in cell i by $C_c(x_i)$, which depends on the invasion area, x_i.

$C_s(S_i)$ represents the cost ($) of search. Search effort, S_i, corresponds to the number of labor-hours spent searching for the specific species in cell i.

Hence, the total costs can be expressed as

$$E(C_i) = D(x_i) + C_s(S_i) + C_c(x_i)$$

Usually, the timber industry harvests pine trees every 25 years and pulpwood trees every 15 years, with all aboveground plant species also being removed. Hence, I assumed there would be a timber harvest every 20 years and added 20-year time frame into the expected costs in forest productivity, which are given by:

$$E(C_i) = \sum_{0}^{20} \frac{1}{(1+r)^t}[D(x_i(t)) + C_s(S_i(t))] + \sum_{j=1}^{n} \frac{1}{(1+r)^{t_j}} C_c(x_i(t_j))$$

where r is the discount rate (5%/year as the base) (Mishkin, 2007), $D(x_i(t))$ is the discounted present value of timber losses ($) in cell i at time t, $C_s(S_i(t))$ is the discounted present value of searching in cell i at time t, $C_c(x_i(t_j))$ is the discounted present value of the control cost for the jth time control in cell i at time t_j.

4.2.2 Estimation of damage costs

From Section 4.2.1, I denoted the damage cost in timber losses by $D(x_i) = x_i \times V_i \times P_i$. Here, x_i is the invaded area (ha) in cell i, which can be estimated

by the dispersal models from the previous section, so there is a need to collect information for estimating timber productivity (V_i) and the market price of timber (P_i).

First, I defined the study area as in the previous section. For Chinese tallow, the study area included East Texas, Louisiana, and part of Mississippi, Arkansas, and Oklahoma. For Chinese and European privets and Japanese honeysuckle, the study area included Mississippi, Alabama, and part of Florida, Georgia, Tennessee, Arkansas, and Louisiana.

Next, I collected timber productivity data for five major timber products (pine sawtimber, pine chip-n-saw, pine pulpwood, mixed hardwood sawtimber, mixed hard wood pulpwood) in each state from Forest Service data (Bentley *et al.*, 2005; Johnson *et al.*, 2007; Bentley *et al.*, 2008; Johnson *et al.*, 2008a, b; Xu, 2008; Howell and Johnson, 2009; Johnson *et al.*, 2009a; Mathison and Schnabel, 2009; Schiller and Hendricks, 2009) and TPO data (USDA, 2007b) (Table 9). This information describes the timber productivity by volume. Units of timber price data from Timber Mart-South data are $/ton (TMS, 2009). Hence, I converted the data in Table 9 to tons by assuming that 1 short ton (2,000 lb.) of green southern pine, wood and bark, has about 0.822 cubic meter of solid wood and 1 short ton of green mixed hardwood, wood and bark, has about 0.787 cubic meter of solid wood (Johnson *et al.*, 2008b) (Table 10). I then calculated the average production per acre (ton/acre) by using the values in Table 10 by dividing the corresponding numbers of acres of timberland (Table 11). Here, I decided to spread each of the five timber productions evenly acres all the cells of forest industry land in the simulation model. This is because: (1) data on timber production at a finer spatial scale

Table 9. Annual removals of growing stock (million cubic meters) on timberland in Alabama (AL), Mississippi (MS), Louisiana (LA), Texas (TX), Arkansas (AR), Florida (FL), Georgia (GA), Oklahoma (OK), and Tennessee (TN) by class of timber in 2006 (USDA, 2007b).

State	AL	MS	LA	TX	AR	FL	GA	OK	TN
Softwoods	25.15	21.29	19.74	16.14	14.05	13.33	30.64	2.27	2.86
Hardwoods	11.61	11.24	7.39	5.64	8.50	8.50	10.36	1.53	8.01

Table 10. Annual removals of growing stock (million tons) on timberland in Alabama (AL), Mississippi (MS), Louisiana (LA), Texas (TX), Arkansas (AR), Florida (FL), Georgia (GA), Oklahoma (OK), and Tennessee (TN) by class of timber in 2006.

State	AL	MS	LA	TX	AR	FL	GA	OK	TN
Softwoods	30.59	25.91	24.01	19.64	17.09	16.23	37.27	2.76	3.48
Hardwoods	14.75	14.28	9.39	7.16	10.79	3.24	13.17	1.94	10.19

Table 11. Annual growing stock (ton/acre) on timberland in Alabama (AL), Mississippi (MS), Louisiana (LA), Texas (TX), Arkansas (AR), Florida (FL), Georgia (GA), Oklahoma (OK), and Tennessee (TN) by class of timber (Smith *et al.*, 2004).

State	AL	MS	LA	TX	AR	FL	GA	OK	TN
Softwoods	8.18	8.00	6.16	5.28	3.80	4.04	8.51	2.63	2.50
Hardwoods	3.94	4.41	2.41	1.92	2.40	0.81	3.01	1.86	7.32

(each cell represent approximately 6,000 acres) are not available. (2) Timber industry harvests different stands each year, but the production is similar among stands (Johnson *et al.*, 2008b). Next, I calculated the average market price of timber from the year 2000 to 2008 based on data from Timber Mart-South (2009) (Table 12). Finally, I calculated the average timber value per acre ($/acre) using the information in Tables 11 and 12 (Table 13).

4.2.3 Estimation of control and searching costs

To estimate appropriate control and searching costs, I interviewed five invasion plant control companies: (1) BASF - The Chemical Company, (2) ChemPro Service, Inc., (3) Marshfield Forest Service, Inc., (4) Progressive Solutions, and (5) Superior Forestry Service, Inc. I chose these companies because they have licenses and work in different parts of the study region and other region including Arkansas, Delaware, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Missouri, Nebraska, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Virginia, and West Virginia. I interviewed the staffs who worked in these companies through phone calls during the period from July 15 to 21, 2009 and recorded their estimates of how much the control and searching costs would be for different invasive species and for different invasion intensities (Table 14).

Usually, people request invasion control services when they are aware of an invasion, so search costs are included in control cost estimates and seldom are estimated separately. However, I did obtain an estimate of searching cost from Progressive

Table 12. Average stumpage prices ($/ton) from 2000 to 2008 in the southern United States (TMS, 2009).

Year	2000	2001	2002	2003	2004	2005	2006	2007	2008	Average
Softwoods	71.28	65.01	65.38	65.43	67.64	70.51	66.94	64.58	57.32	66.00
Hardwoods	22.28	23.92	23.88	27.18	26.68	28.50	26.72	28.53	27.88	26.18

Table 13. Annual growing stock value ($/acre) on timberland in Alabama (AL), Mississippi (MS), Louisiana (LA), Texas (TX), Arkansas (AR), Florida (FL), Georgia (GA), Oklahoma (OK), and Tennessee (TN) by timber product.

State	AL	MS	LA	TX	AR	FL	GA	OK	TN
Softwoods	583.02	520.11	402.73	345.37	257.00	284.84	569.53	169.99	143.38
Hardwoods	87.88	105.52	57.53	52.32	64.04	22.98	80.32	52.94	204.09
Total price/acre	670.90	625.63	460.26	397.69	321.04	307.83	649.85	222.93	347.47

Table 14. Estimates of control costs ($/acre) based on phone interviews with five invasive plant control companies during the period from July 15 to 21, 2009.

Company	Interview Date	General price range for all invasive plant species					
Marshfield Forest Service, Inc.	7/15/2009	$10-$400					
ChemPro Services, Inc.	7/16/2009	$150-$500					
BASF-The Chemical Company	7/21/2009	$50-$400					
Progressive Solutions	7/16/2009	Detailed price range by invasion intensity for all invasive plant species					
		<5%	5%-20%	20%-40%	40%-60%	60%-80%	80%-100%
		$10-$25	$25-$75	$75-$130	$130-$200	$200-$300	$300-$450
Superior Forestry Service, Inc.	7/21/2009	Detailed price range by invasion intensity for my focus invasive plant species					
		Species			<25%	25%-60%	60%-100%
		Chinese tallow			$45-$85	$85-$185	$185-$585
		Chinese and European privets			$50-$100	$100-$250	$250-$650
		Japanese honeysuckle			$75-$150	$150-$300	$300-$800

Solutions, which provides this service for $8/acre.

4.2.4 Projecting expected costs in forest productivity

I projected the expected costs in forest productivity over the next 20 years of Chinese tallow, Chinese and European privets, and Japanese honeysuckle, under four different scenarios, including (1) no control (NOC), (2) control beginning when invasion intensity reaches 60% (low control intensity, LOWC), (3) control beginning when invasion intensity reaches 25% (medium control intensity, MEDC), and (4) control beginning immediately (as soon as invasion intensity greater than zero, high control intensity, HIGHC) using the simulation process described in Fig. 35.

I defined the thresholds for the low, medium, and high intensity controls based on the interview information on control costs and search costs (Table 14). I used the average control costs from Superior Forestry Service, Inc., since this company offered more specific price estimated for each of the invasive plant species: 65, 135, and 385 ($/acre) for controlling Chinese tallow, 75, 175, and 450 ($/acre) for controlling Chinese and European privets, and 112.5, 225, and 550 ($/acre) for controlling Japanese honeysuckle in low, middle, and high intensity invasions, respectively, with a searching cost of 8 ($/acre). Also, I used the average growing stock ($/acre) for the damage cost (Table 13) and applied different discount rates: 1%, 3%, 7%, and 9% for checking influences.

I projected expected costs in forest productivity using the cost equations described earlier, modified to include the reduction of the percentage land cover of

invasive species to zero in cells meeting the control criterion, and the associated economic costs of search and control (Fig. 35). As before, I exported the geo-referenced simulated data to ArcView® and Excel to visualize spatial patterns and analyze the economic losses.

4.3 Results

The predicted spread of Chinese tallow by my model over the next 20 years under low intensity control in East Texas and Louisiana was slower than the spread with no control, however, the invasion would still spread gradually from the region close to the Gulf of Mexico northward and westward into the forests of Arkansas (Figs. 36) under the low intensity control scenario. The spread projected under medium intensity control indicated that there was no severely invaded area (maximum invasion intensity $< 50\%$), but the invasion expanded to Arkansas (Fig. 37). The spread projected under high intensity control indicated that the invasion intensity of most invaded areas was less than 25% and the invasion was limited to the area around the Gulf of Mexico (Fig. 38).

The spread of Chinese and European privets projected under low intensity control in Mississippi and Alabama did not exhibit severely invaded ($> 75\%$) areas as the spread with no control, but the invasion generally would spread over the same area (Fig. 39). The spread projected under medium intensity control exhibited no severely invaded (maximum invasion intensity $< 50\%$) areas, and the invasion did not extend much beyond its initial area (Fig. 40). The spread projected under high intensity control

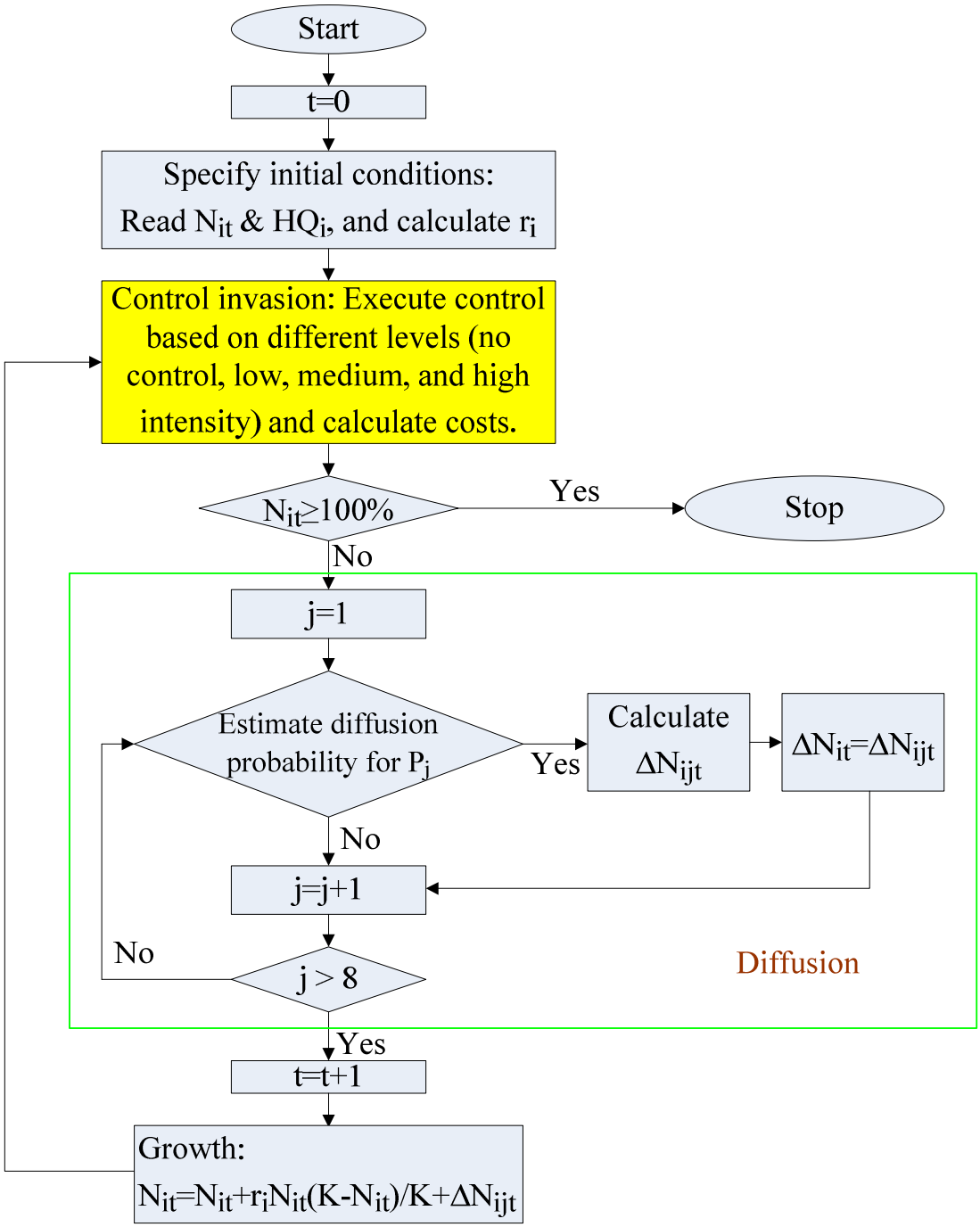


Fig. 35. Flow chart of the modified version of the simulation model used to project expected total costs.

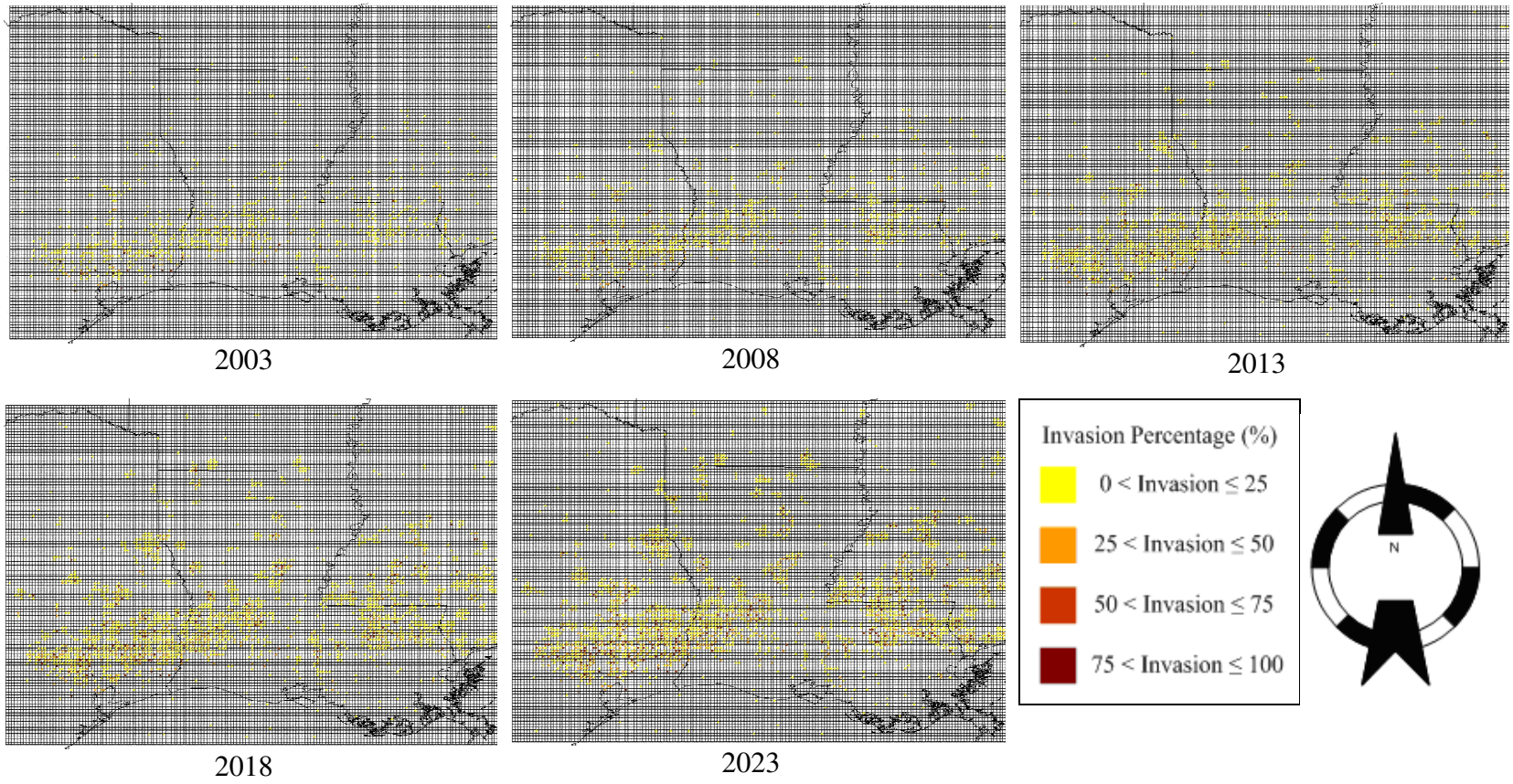


Fig. 36. Observed pattern of Chinese tallow invasion in the year 2003 based on the nonnative invasive plant dataset (USDA, 2008b) and simulated patterns of Chinese tallow invasion under low intensity control between the years 2003 and 2023 based on one randomly-chosen stochastic simulation.

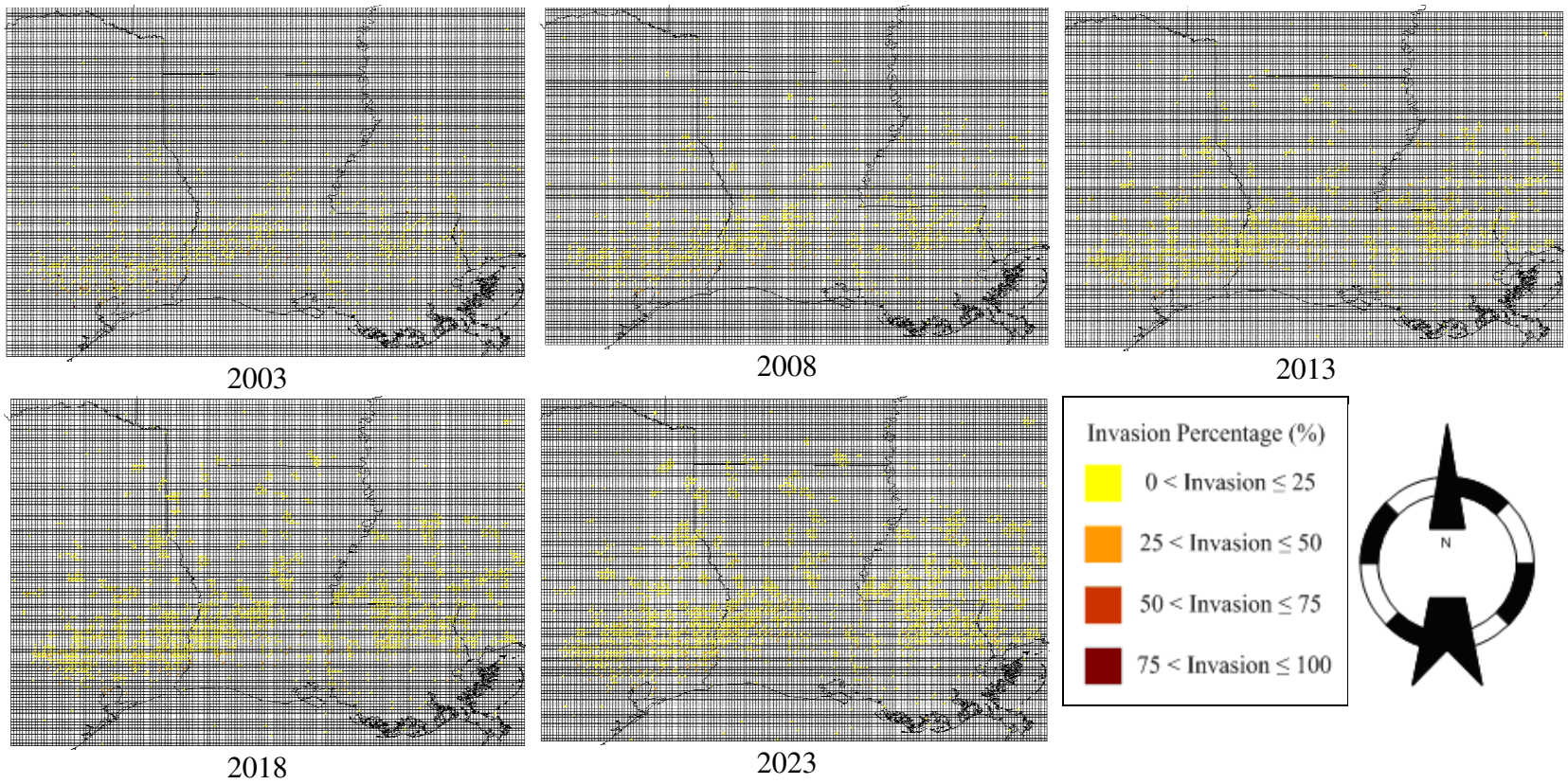


Fig. 37. Observed pattern of Chinese tallow invasion in the year 2003 based on the nonnative invasive plant dataset (USDA, 2008b) and simulated patterns of Chinese tallow invasion under medium intensity control between the years 2003 and 2023 based on one randomly-chosen stochastic simulation.

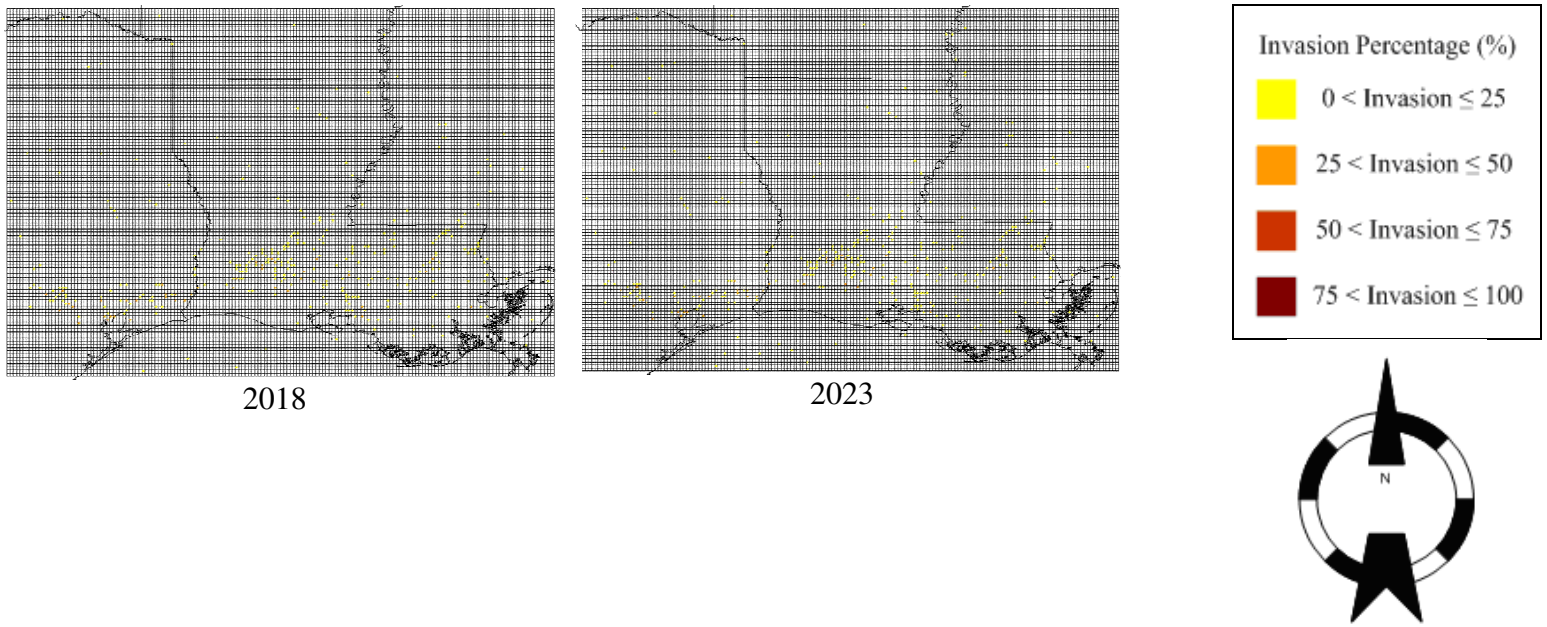


Fig. 38. Observed pattern of Chinese tallow invasion in the year 2003 based on the nonnative invasive plant dataset (USDA, 2008b) and simulated patterns of Chinese tallow invasion with control immediately between the years 2003 and 2023 based on one randomly-chosen stochastic simulation.

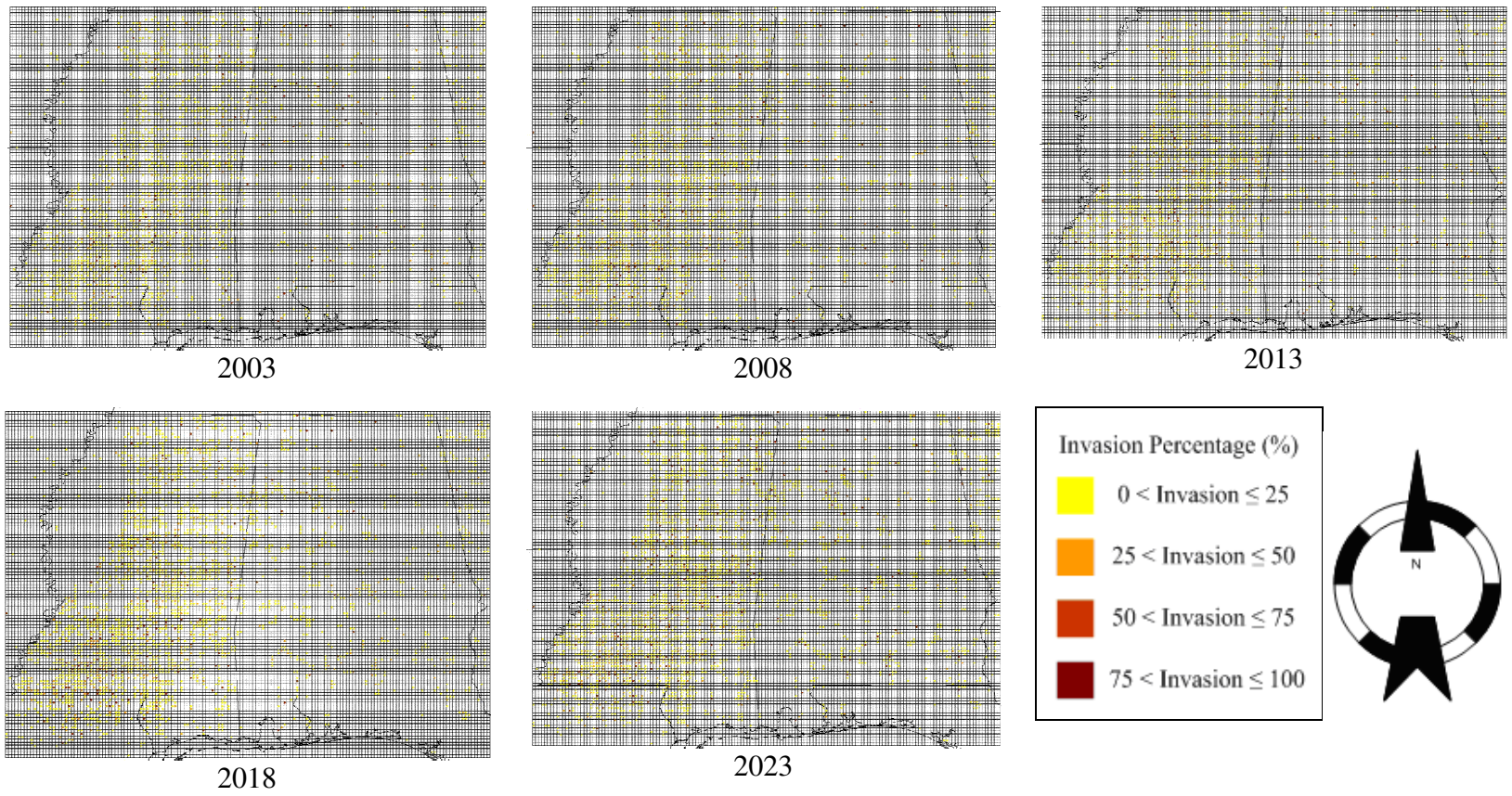


Fig. 39. Observed pattern of Chinese and European privets invasion in the year 2003 based on the Nonnative invasive plant dataset (USDA, 2008b) and simulated patterns of Chinese tallow invasion under low intensity control between the years 2003 and 2023 based on one randomly-chosen stochastic simulation.

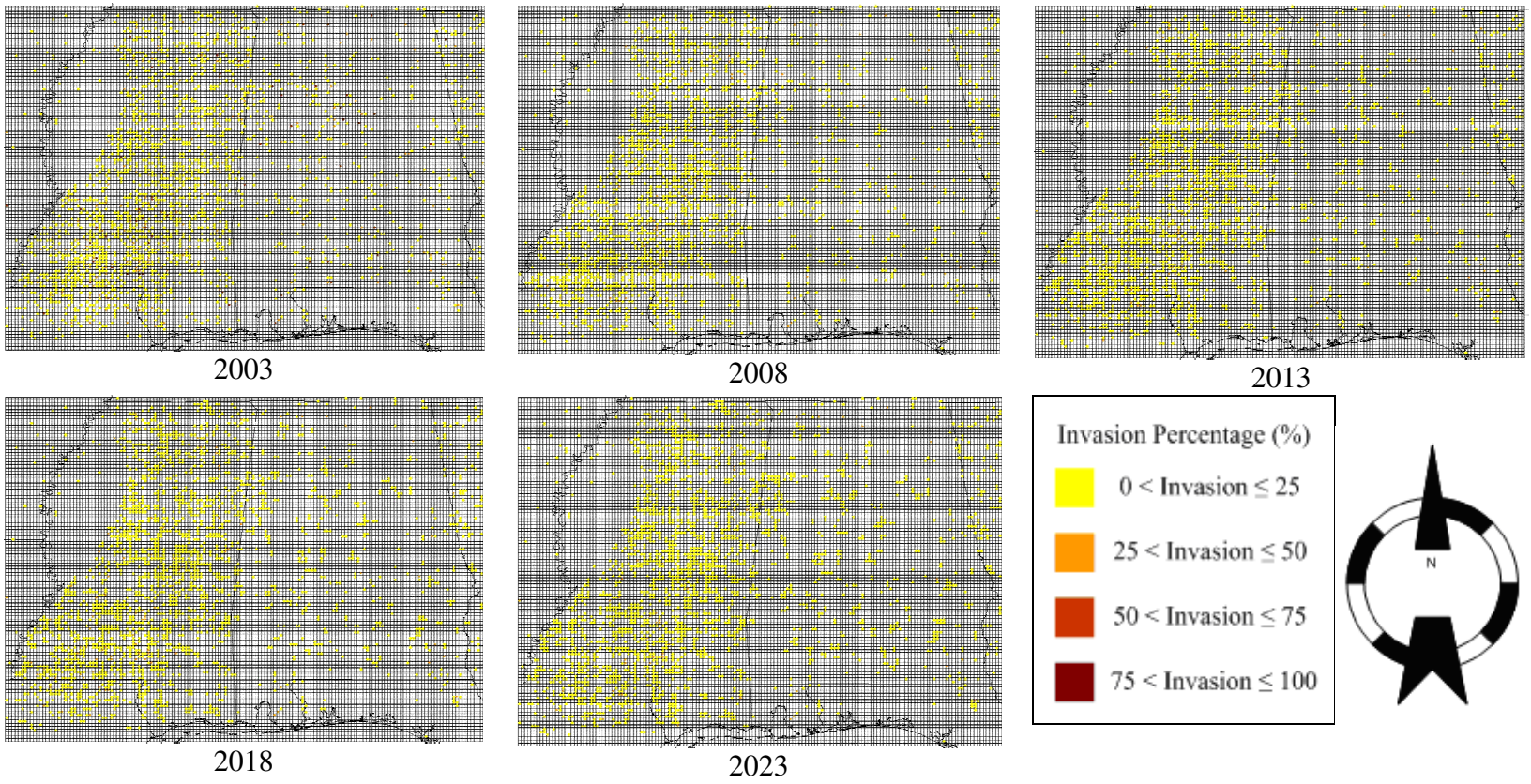


Fig. 40. Observed pattern of Chinese and European privets invasion in the year 2003 based on the Nonnative invasive plant dataset (USDA, 2008b) and simulated patterns of Chinese and European privets invasion under medium intensity control between the years 2003 and 2023 based on one randomly-chosen stochastic simulation.

indicated that the invasion intensity of most invaded areas was less than 25% and the invaded area decreased dramatically over the 20 years (Fig. 41).

The spread of Japanese honeysuckle projected under low intensity control in Mississippi and Alabama exhibited fewer severely invaded (> 75%) area as the invasion with no control, but the invasion would still gradually spread southward (Fig. 42). The spread projected under medium intensity control exhibited no severely invaded (maximum invasion intensity < 50%) areas, and the invaded area gradually decreased (Fig. 43). The spread projected under high intensity control indicated that the invasion intensity of most invaded areas was less than 25% and the invaded area decreased dramatically over the 20 years (Fig. 44).

Projection of invasion of Chinese tallow in East Texas and Louisiana with no control indicated that the invaded area increased exponentially. The invaded area also increased exponentially under low intensity control, but at a slower rate than with no control. Under medium intensity control, the invaded area again increased exponentially, but at an even slower rate than under previous conditions. Under high intensity control, the invaded area decreased dramatically in the year 2005 (from 164,474 to only 307 acres on 51.77 million acres of forest land) (Fig. 45).

Projection of invasion of Chinese and European privets in Mississippi and Alabama with no control indicated that the invaded area increased exponentially. Under low intensity control, the invaded area increased linearly, but slower than with no control. Under medium intensity control, the invaded area decreased dramatically in the year 2005, and then remained stable between 400 to 600 thousand acres. Under high

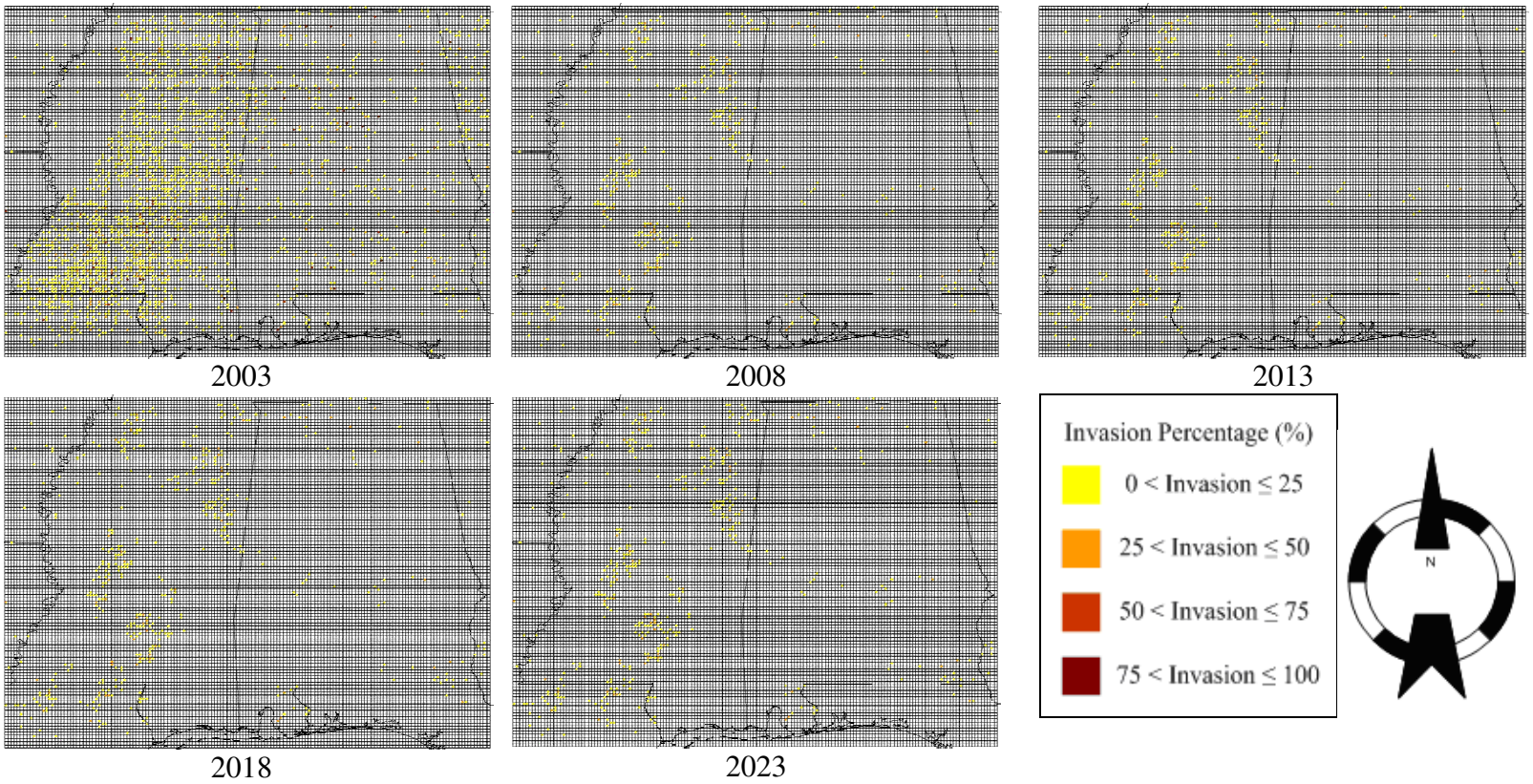


Fig. 41. Observed pattern of Chinese and European privets invasion in the year 2003 based on the Nonnative invasive plant dataset (USDA, 2008b) and simulated patterns of Chinese and European privets invasion with control immediately between the years 2003 and 2023 based on one randomly-chosen stochastic simulation.

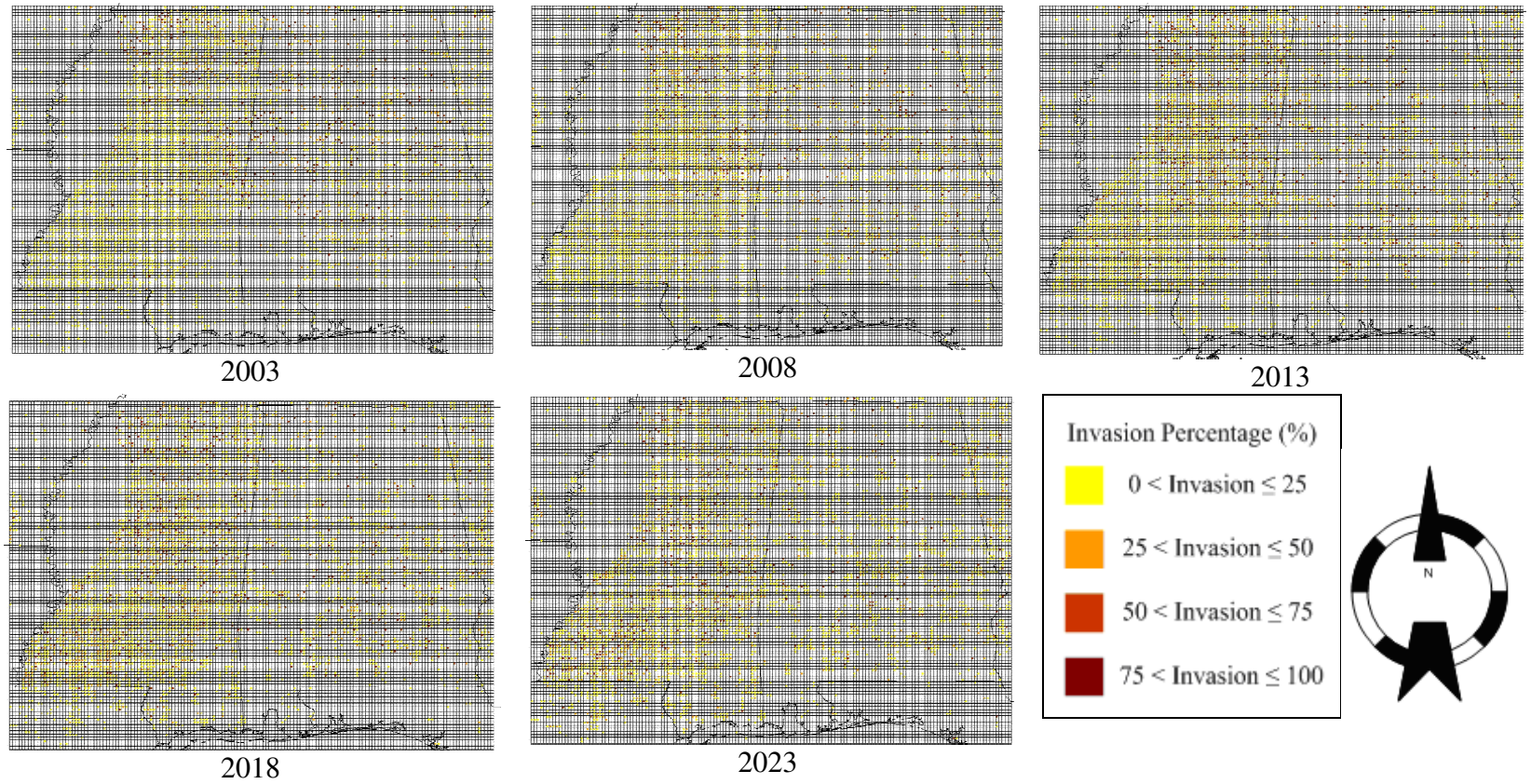


Fig. 42. Observed pattern of Japanese honeysuckle invasion in the year 2003 based on the Nonnative invasive plant dataset (USDA, 2008b) and simulated patterns of Japanese honeysuckle under low intensity control between the years 2003 and 2023 based on one randomly-chosen stochastic simulation.

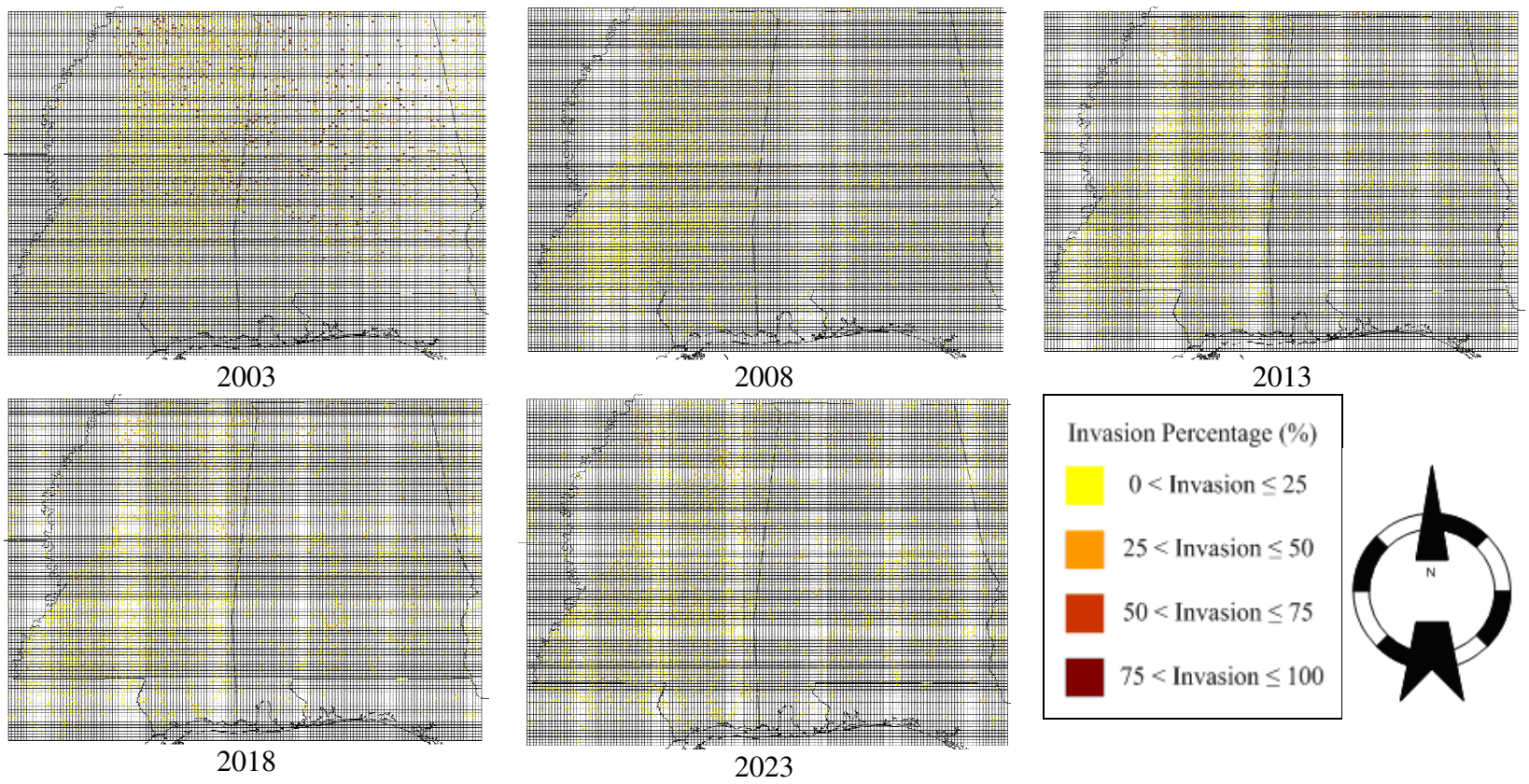


Fig. 43. Observed pattern of Japanese honeysuckle invasion in the year 2003 based on the Nonnative invasive plant dataset (USDA, 2008b) and simulated patterns of Japanese honeysuckle invasion under medium intensity control between the years 2003 and 2023 based on one randomly-chosen stochastic simulation.

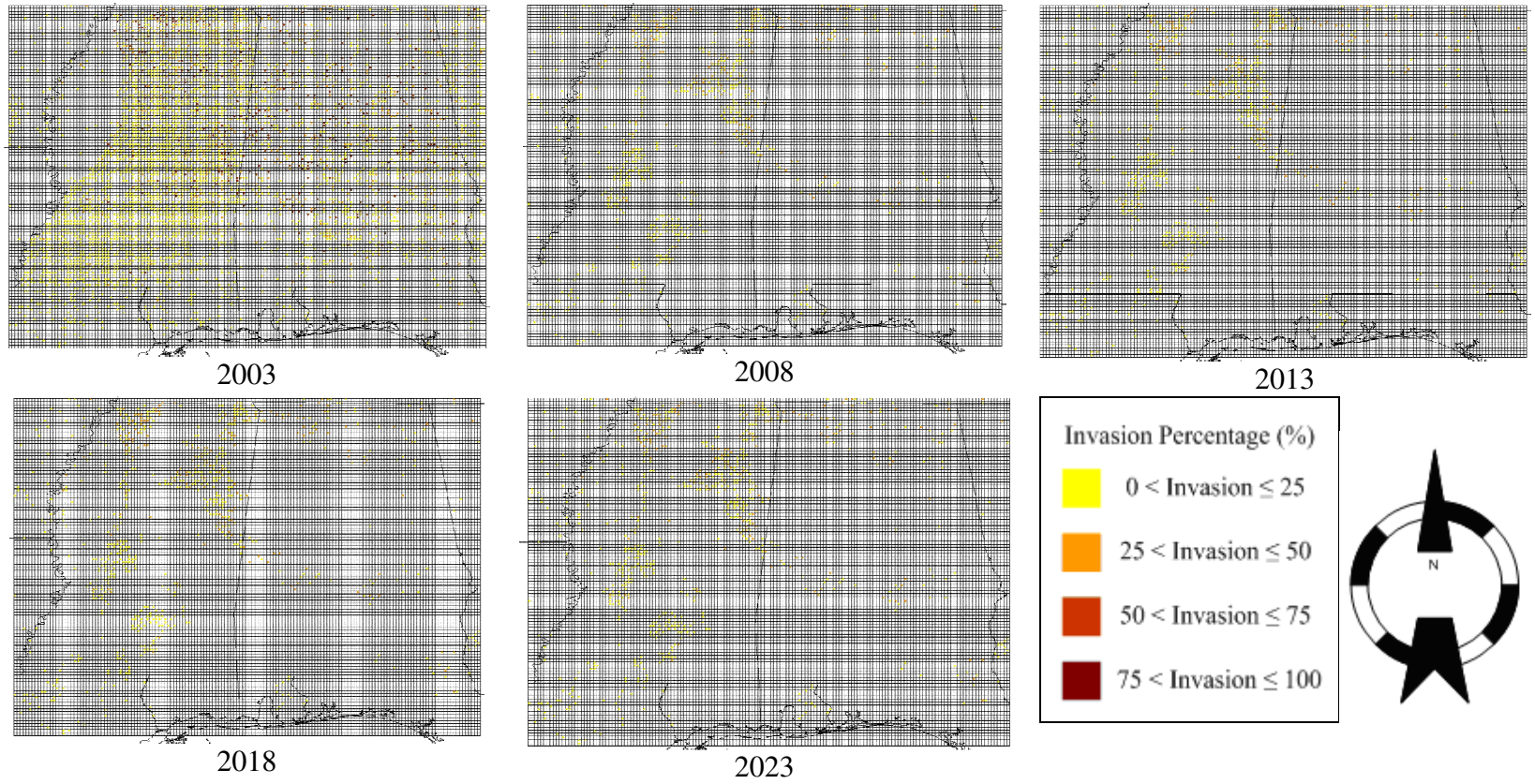


Fig. 44. Observed pattern of Japanese honeysuckle invasion in the year 2003 based on the Nonnative invasive plant dataset (USDA, 2008b) and simulated patterns of Japanese honeysuckle invasion with control immediately between the years 2003 and 2023 based on one randomly-chosen stochastic simulation.

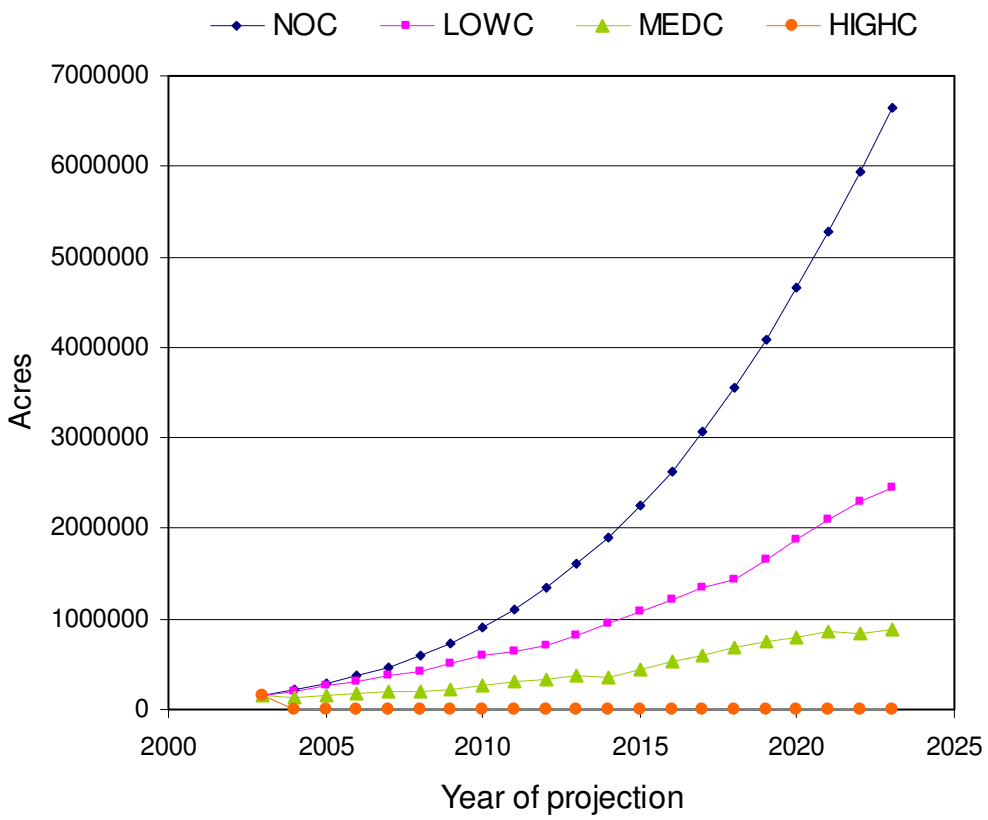


Fig. 45. The invaded area (acres) for the four different control levels for Chinese tallow in East Texas and Louisiana.

intensity control, the invaded area decreased dramatically in the year 2005 (from 823,309 to 95 acres) and then remained at a low level (around 100 acres on 67.45 million acres of forest land) (Fig. 46).

Projection of invasion of Japanese honeysuckle in Mississippi and Alabama with no control indicated that the invaded area increased exponentially. Under low intensity control, the invaded area increased more slowly than with no control, and reached a stable level (around 3.25 million acres) in the year 2014. Under medium intensity control, the invaded area decreased dramatically in the year 2005, and then decreased linearly. Under high intensity control, the invaded area decreased dramatically in the year 2005 (from 2,547,746 to 269 acres), and then remained at a low level (around 300 acres on 67.45 million acres of forest land) (Fig. 47).

Projection of invasion of Chinese tallow in East Texas and Louisiana with no control indicated that annual expected costs in forest productivity increased exponentially for 1%, 3%, and 5% discount rates. When the discount rates equaled 7% and 9%, annual expected costs initially decreased, but started increasing exponentially in the year 2011 and 2016 (Fig. 48a). Annual expected costs increased exponentially, but a slower rate than with no control for 1%, 3%, and 5% discount rates under low intensity control. When the discount rates equaled 7% and 9%, annual expected costs initially decreased, but started increasing exponentially in the year 2019 (Fig. 48b). Under medium intensity control, annual expected costs increased linearly for 1% and 3% discount rates, but decreased linearly for 5%, 7%, and 9% discount rates (Fig. 48c). Under high intensity control, annual expected costs were very high in the year 2004,

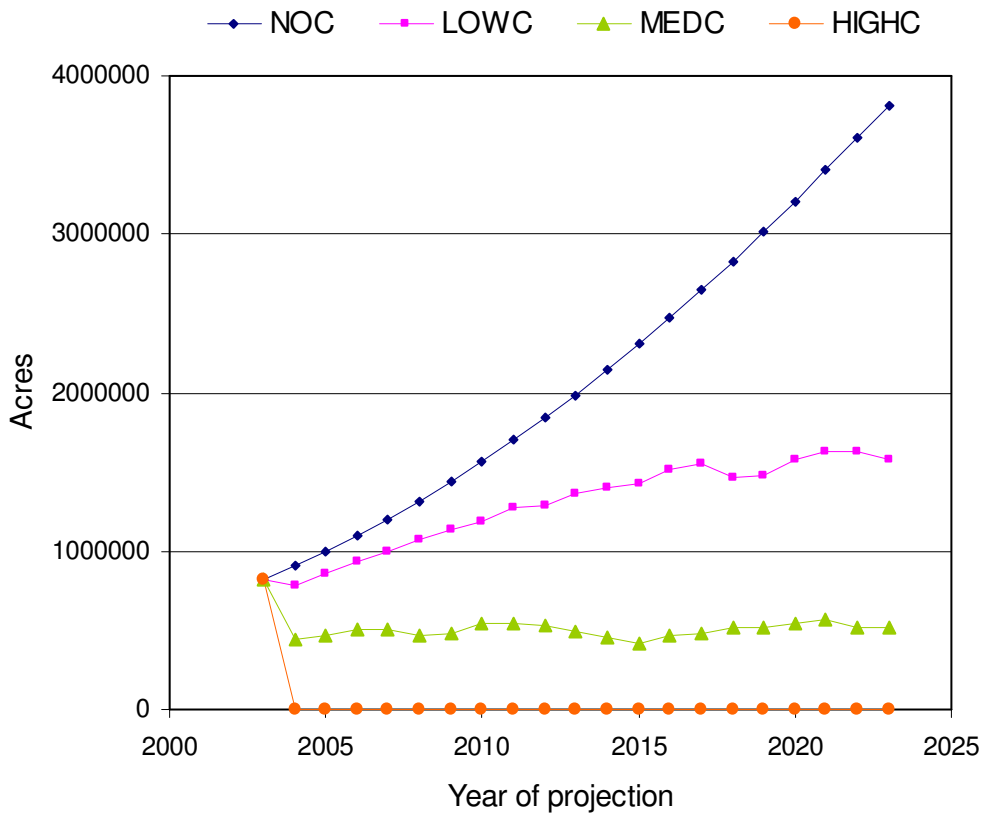


Fig. 46. The invaded area (acres) for the four different control levels for Chinese and European privets in Mississippi and Alabama.

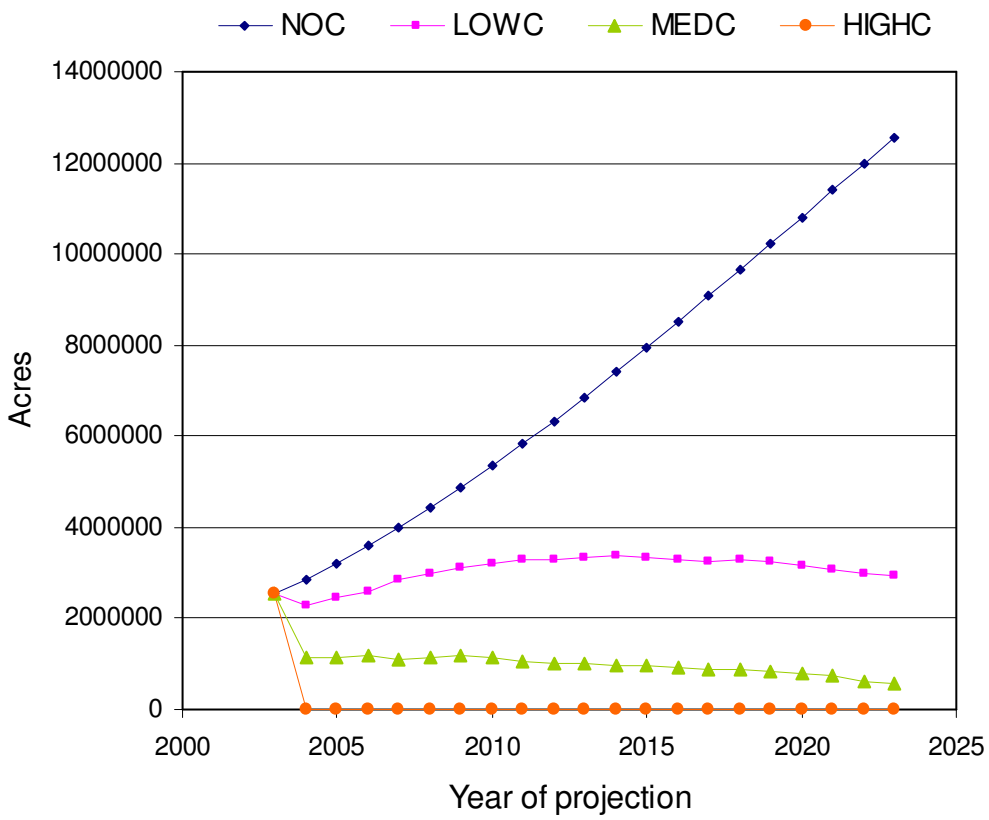
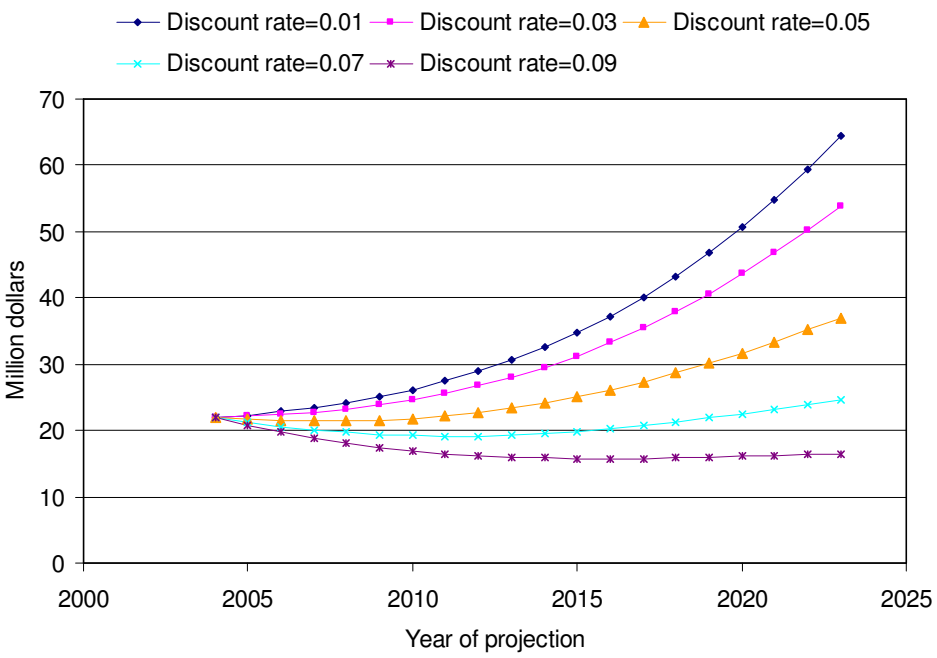


Fig. 47. The invaded area (acres) for the four different control levels for Japanese honeysuckle.

a



b

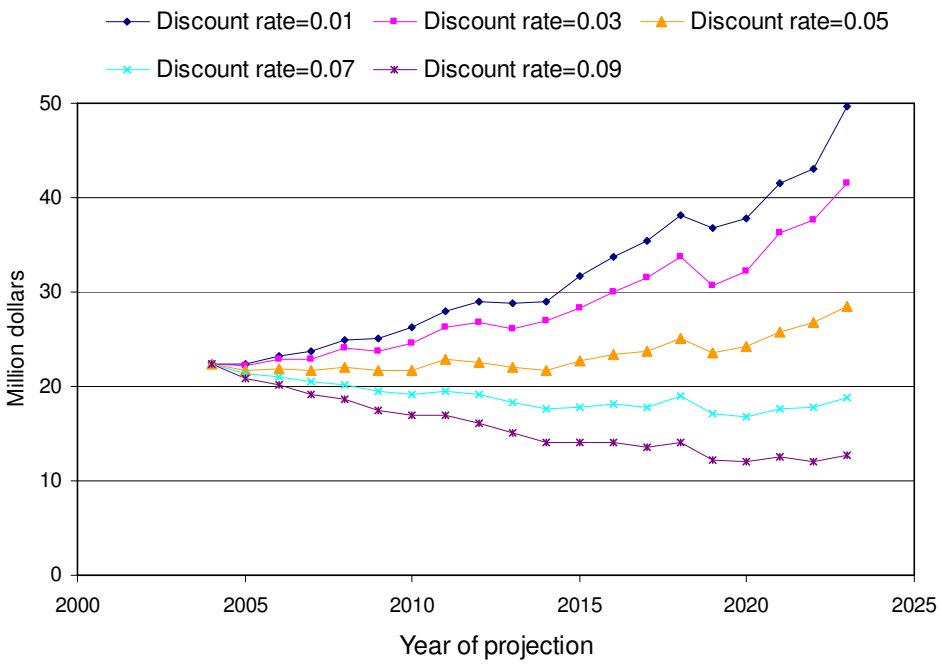
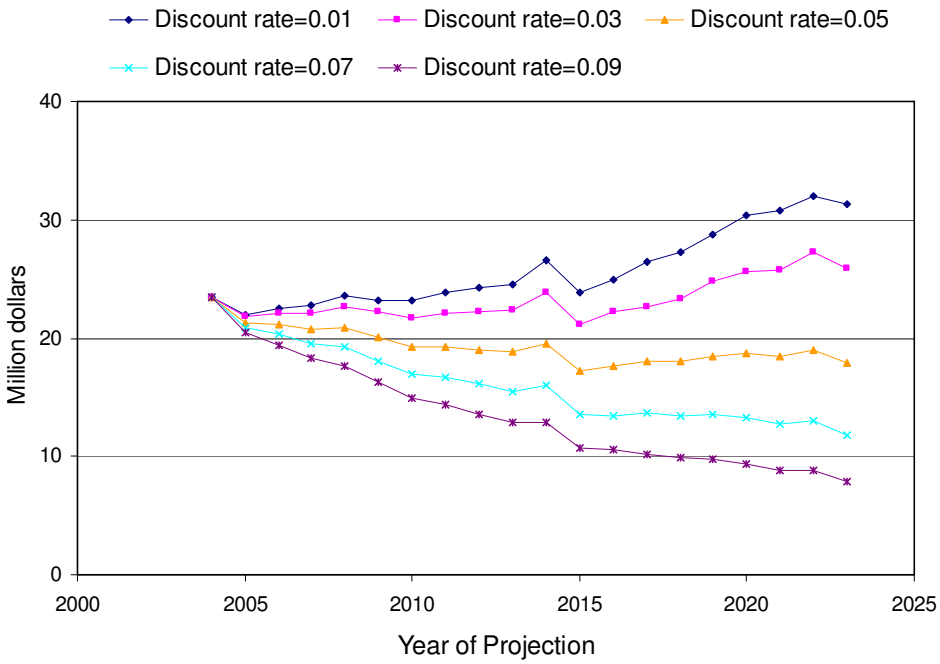


Fig. 48. Annual expected costs (million dollars) in forest productivity for 1%, 3%, 5%, 7%, and 9% discount rates under four different control levels for Chinese tallow in East Texas and Louisiana. a) No control, b) low intensity control, c) medium intensity control, and d) high intensity control.

c



d

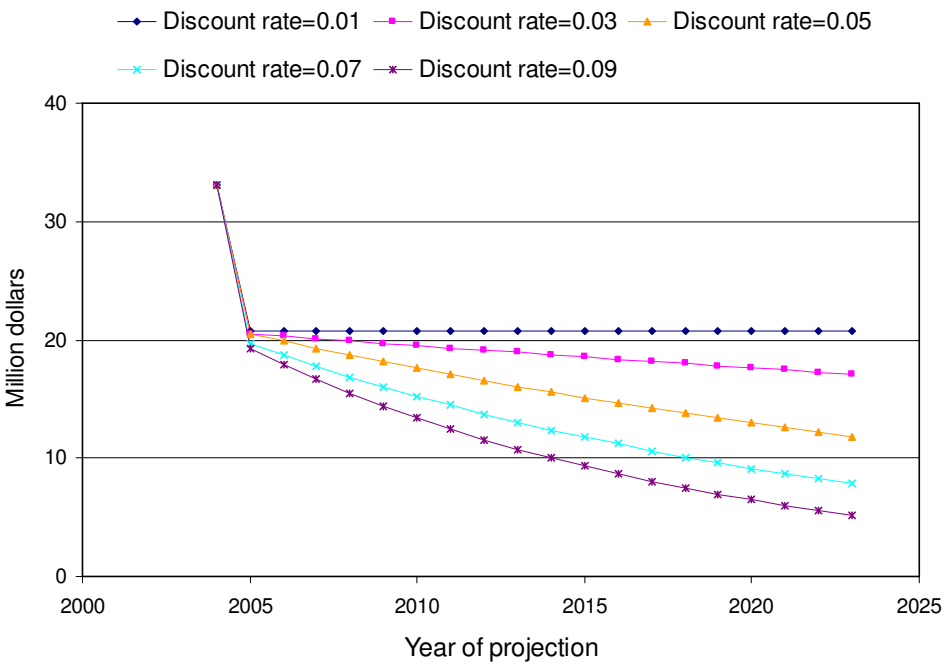


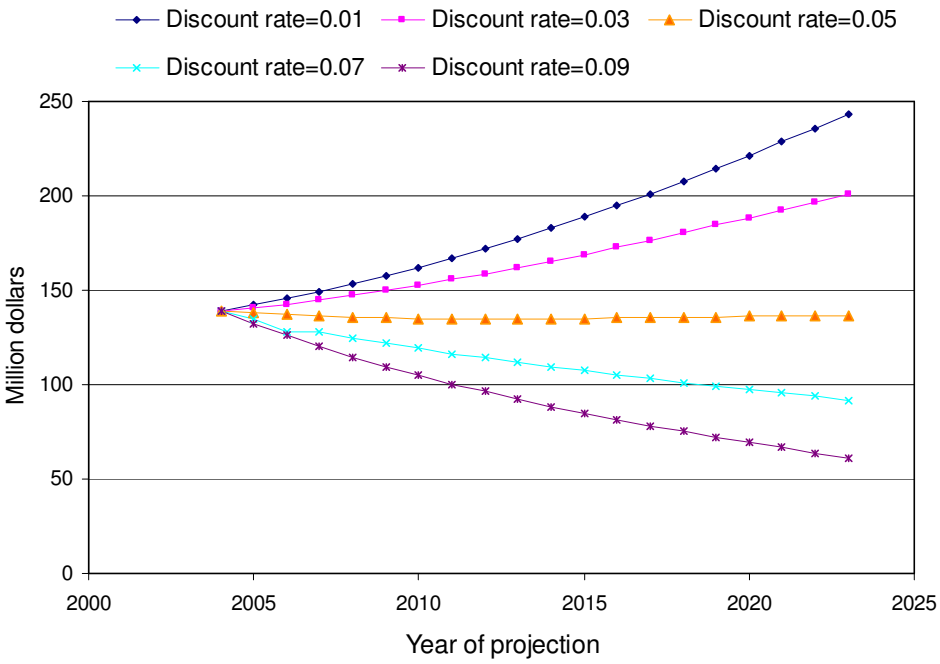
Fig. 48. continued.

kept constant (around 21 million dollars) for 1% discount rate, and decreased linearly for 3%, 5%, 7%, and 9% discount rates (Fig. 48d).

Projection of invasion of Chinese and European privets in Mississippi and Alabama with no control indicated that annual expected costs in forest productivity increased exponentially for 1% and 3% discount rates, remained constant around 135 million dollars for 5% discount rate, and decreased linearly for 7% and 9% discount rates (Fig. 49a). Annual expected costs increased for 1% and 3% discount rates, and decreased linearly for 5%, 7%, and 9% discount rates under low intensity control (Fig. 49b). Under medium intensity control, annual expected costs decreased dramatically in the year 2005 for five discount rates, kept constant (around 130 million dollars) for 1% discount rate, and decreased linearly for 3%, 5%, 7%, and 9% discount rates (Fig. 49c). Under high intensity control, annual expected costs were very high in the year 2004, and then kept constant (around 108 million dollars) for 1% discount rate, and decreased linearly for 3%, 5%, 7%, and 9% discount rates (Fig. 49d).

Projection of invasion of Japanese honeysuckle in Mississippi and Alabama with no control indicated that annual expected costs in forest productivity increased linearly for 1%, 3%, and 5% discount rates, kept constant (around 0.45 billion dollars) for 7% discount rate, and decreased for 9% discount rate (Fig. 50a). Annual expected costs increased for 1% and 3% discount rates, and decreased linearly for 5%, 7%, and 9% discount rates under low intensity control after the year 2005 (Fig. 50b). Under medium intensity control, annual expected costs decreased dramatically in the year 2005 for five discount rates, and then decreased for five discount rates (Fig. 50c). Under high

a



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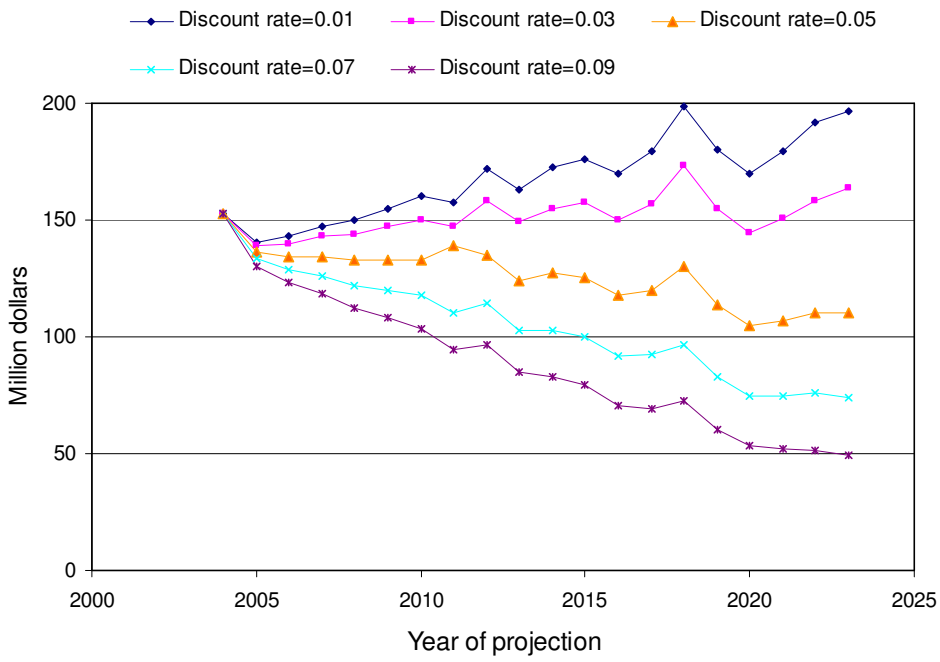
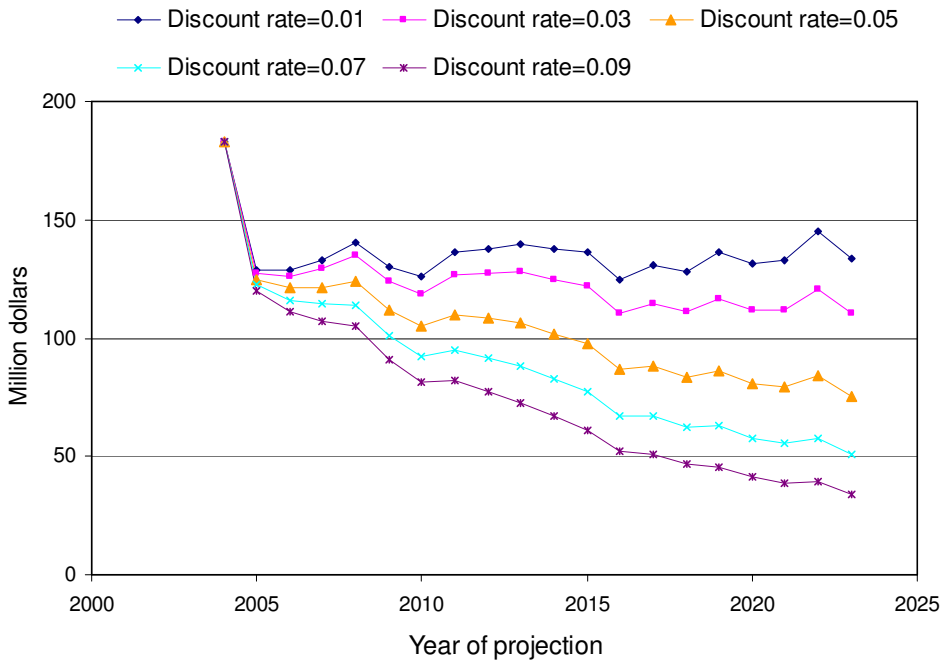


Fig. 49. Annual expected costs (million dollars) in forest productivity for 1%, 3%, 5%, 7%, and 9% discount rates under four different control levels for Chinese and European privets in Mississippi and Alabama. a) No control, b) low intensity control, c) medium intensity control, and d) high intensity control.

c



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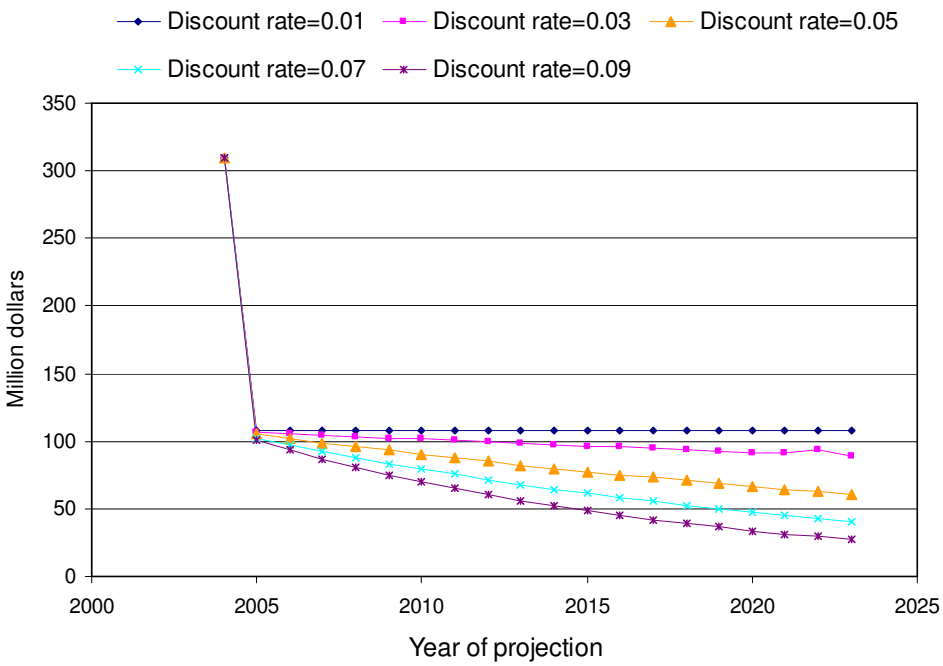
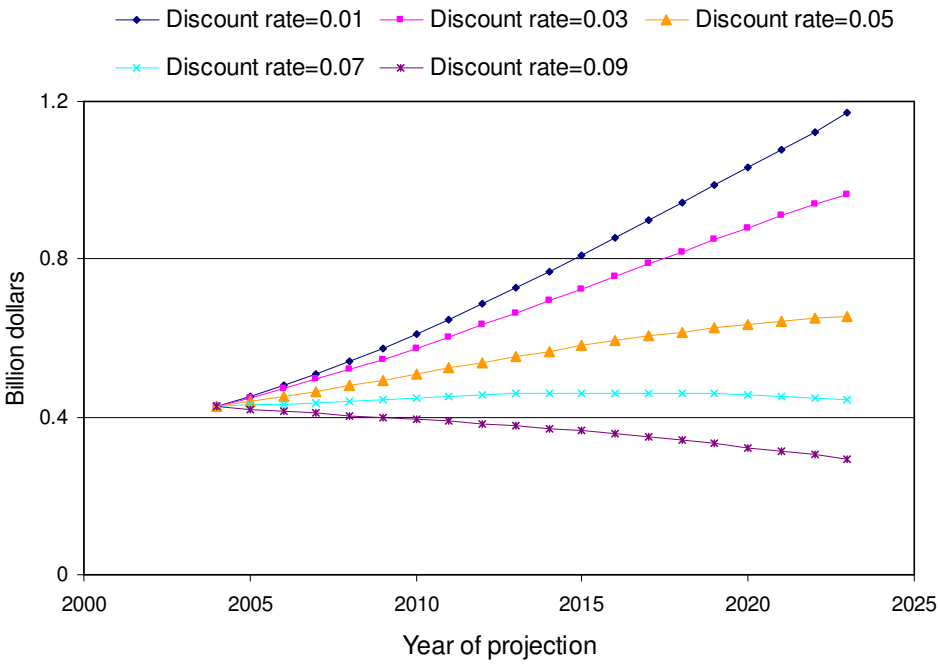


Fig. 49. continued.

a



b

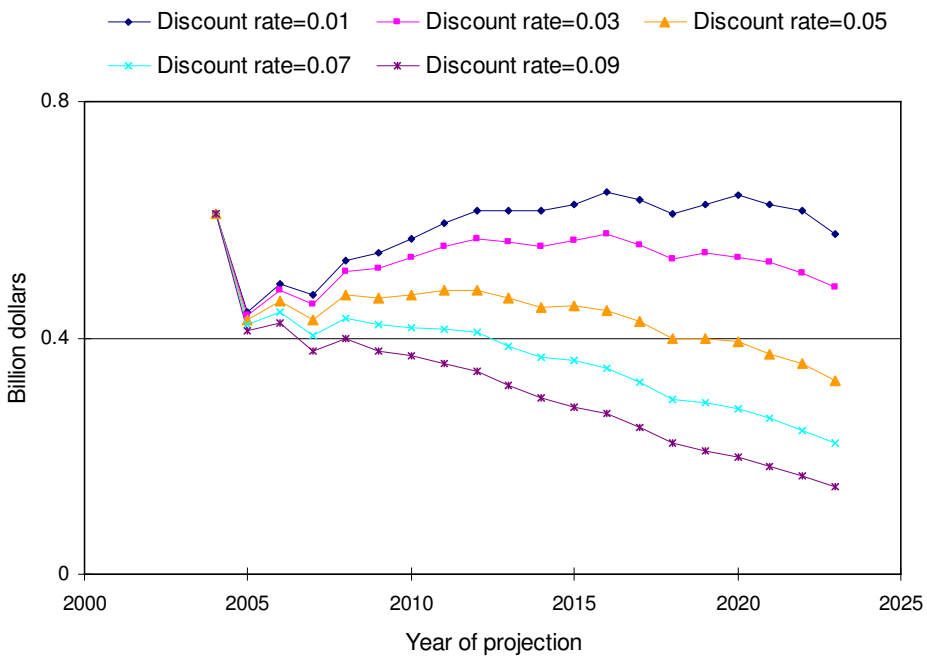
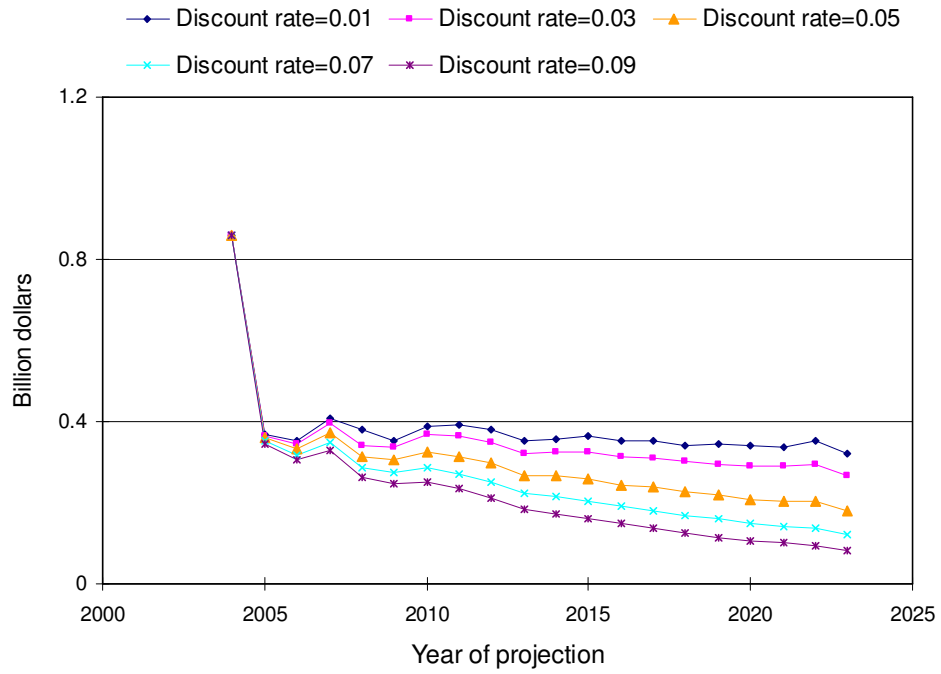


Fig. 50. Annual expected costs (million dollars) in forest productivity for 1%, 3%, 5%, 7%, and 9% discount rates under four different control levels for Japanese honeysuckle in Mississippi and Alabama. a) No control, b) low intensity control, c) medium intensity control, and d) high intensity control.

c



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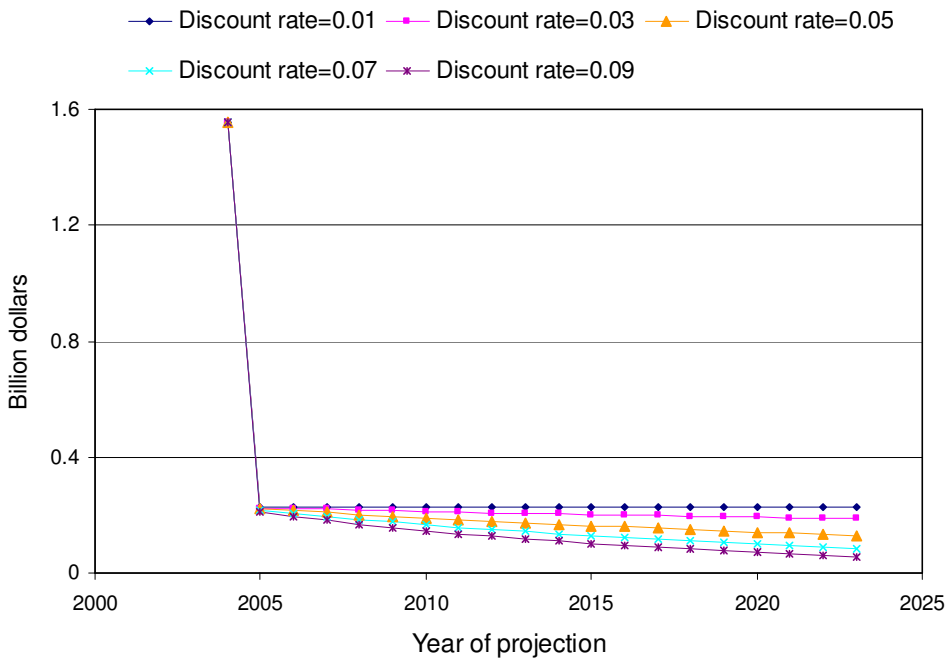

Fig. 50. continued.

intensity control, annual expected costs were very high in the year 2004, and then kept constant (around 0.22 billion dollars) for 1% discount rate, and decreased linearly for 3%, 5%, 7%, and 9% discount rates (Fig. 50d).

4.4 Discussion

4.4.1 Implications of spatial patterns and excepted costs in forest productivity of Chinese tallow, Chinese and European privets, and Japanese honeysuckle under different control scenarios

The spread of Chinese tallow projected by my model over the next 20 years under low and medium control intensities in East Texas and Louisiana was slower than the spread with no control, however, the invasion still expanded gradually into Arkansas. Also, the spread projected under medium control intensity indicated that there was no severely invaded area (maximum invasion intensity < 50%), but the total invaded area in the year 2003 was five times greater than the year 2003 (Figs. 17-21, 36-37, and 45). Thus, it was difficult to control Chinese tallow even under medium control intensity, which provided evidence that Chinese tallow not only has a high growth rate but also great spread dispersal ability. Based on the final invaded area in the year 2023 for Chinese tallow, it appeared that if land owners were willing to apply even low intensity control, they could decrease invasion by more than 60% (Fig. 45).

The spread of Chinese and European privets and Japanese honeysuckle projected by my model over the next 20 years under low control intensity in Mississippi and Alabama was slower than the spread with no control, however, the invasion in the year

2003 still expanded gradually to the same area as with no control, and the invaded area was greater than the year 2003. The spread projected under medium control intensity indicated that there was no severely invaded area, and the total invaded area in the year 2003 was 40% and 80% less, than the year 2003. Thus, landowners could decrease invasions of Chinese and European privets and Japanese honeysuckle even if they only executed medium intensity control. Based on the final invaded area in the year 2023, it appeared that if land owners were willing to apply even low intensity control, they could decrease invasion by more than 40% for Chinese and European privets and 75% for Japanese honeysuckle (Figs. 46 and 47).

Based on expected costs in forest productivity over the 20 years for the five discount rates under the four different control levels for Chinese tallow, Chinese and European privets, and Japanese honeysuckle, it indicated that higher intensity control can decrease more expected costs in forest productivity (Figs. 51, 52, and 53).

4.4.2 Possible improvements

In addition to the model improvements I mentioned in Section 3.4.3, there are several possible improvements for this model. First, the model may underestimate damage costs because I considered decreasing timber productivity as the only damage caused by invasions. However, invasive species do not only decrease forest productivity, but also hinder forest use and management activities, degrade diversity and wildlife habitat, alter the ecosystem (including changes in nutrient cycling, geomorphology and physical structure of the forest stand, drainage patterns and water

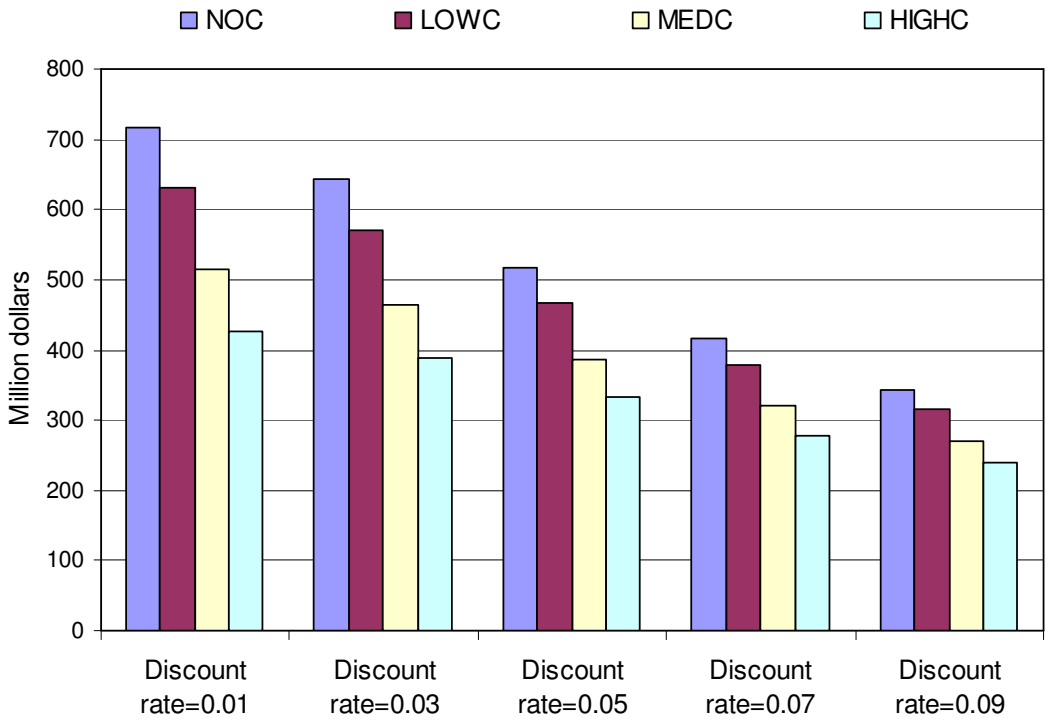

Fig. 51. Expected costs in forest productivity (million dollars) during 20 years for 1%, 3%, 5%, 7%, and 9% discount rates under four different control levels for Chinese tallow in East Texas and Louisiana.

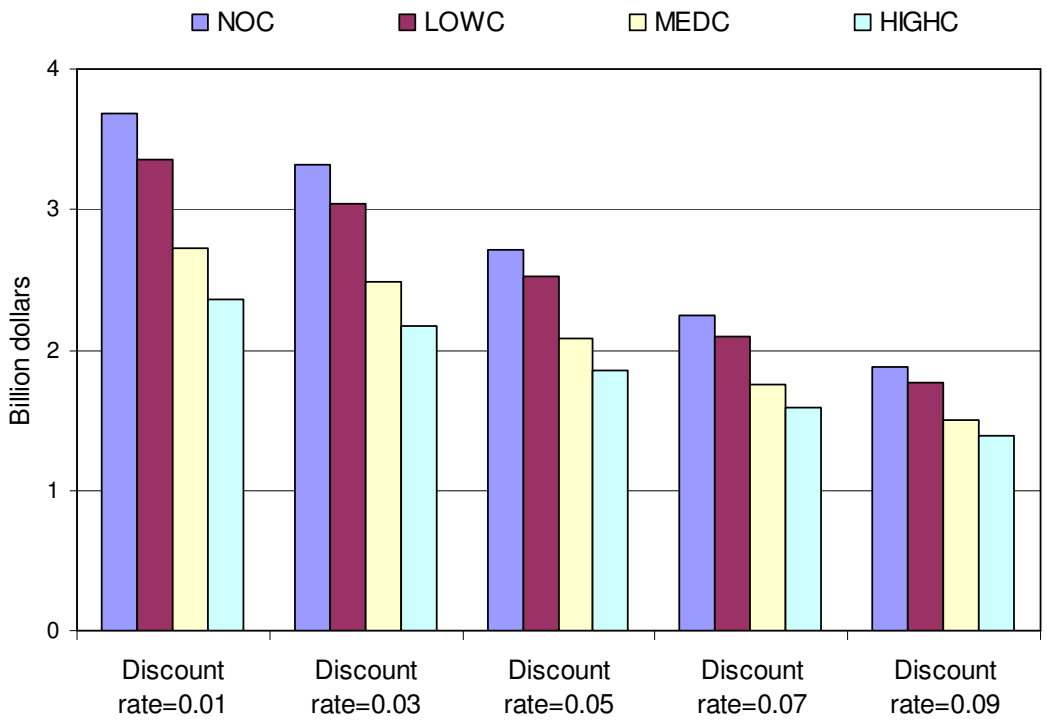

Fig. 52. Expected costs in forest productivity (billion dollars) during 20 years for 1%, 3%, 5%, 7%, and 9% discount rates under four different control levels for Chinese and European privets in Mississippi and Alabama.

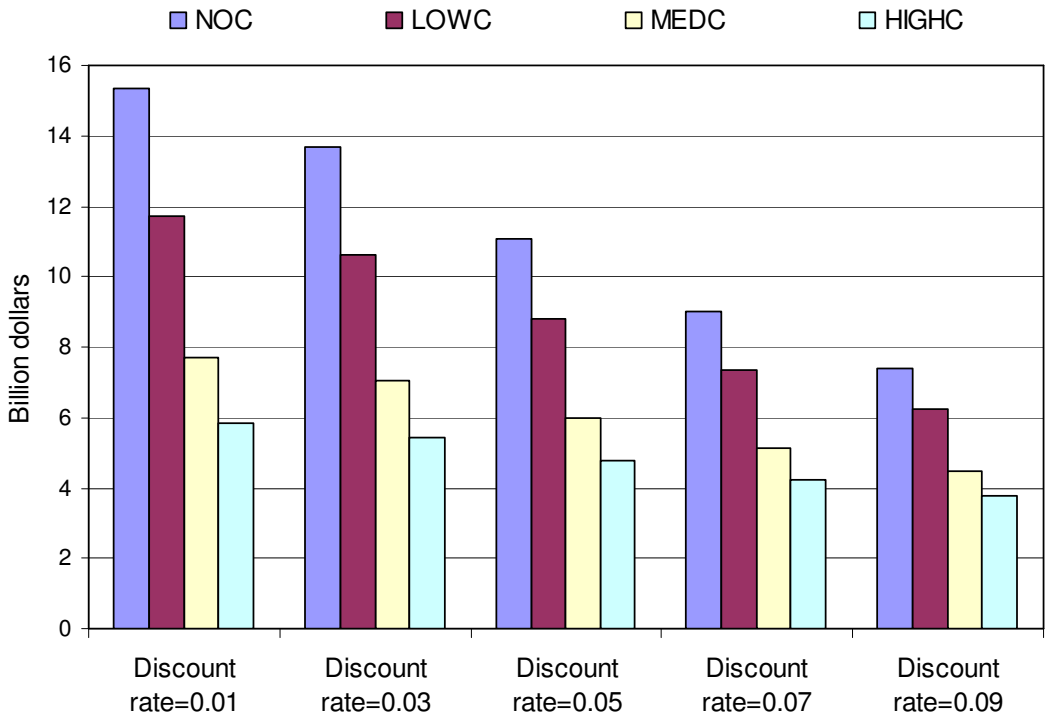

Fig. 53. Expected costs in forest productivity (billion dollars) during 20 years for 1%, 3%, 5%, 7%, and 9% discount rates under four different control levels for Japanese honeysuckle in Mississippi and Alabama.

flow, sedimentation rate, and disturbance regimes) (Reichard and White, 2001). Thus, it is very important to discover appropriate methods (both market and non-market techniques) to take these damages into account.

Second, I only considered damages of the four invasive species. However, they do have several benefits. Chinese tallow is used for beekeeping (Miller, 2003). Seeds and sprouts of Chinese and European privets are great sources of forage for songbirds, the white-tailed deer, the white-footed mouse, and the golden mouse (Miller, 2003; Christopher and Barrett, 2006; Rossell *et al.*, 2007; Wilcox and Beck, 2007). Japanese honeysuckle fruits are great sources of forage for wild turkeys, bobwhites, mockingbirds, white-throated sparrows, white-crowned sparrows, slate-colored juncos, American robins, purple finches, goldfinches, bluebirds, pine grosbeaks, hermit thrushes, house finches, and white-tailed deer (Sheldon and Causey, 1974; Schierenbeck, 2004). Japanese honeysuckle also has value for bank stabilization and erosion control (Miller, 2003; Schierenbeck, 2004). Hence, it will be more appropriate to use cost-benefit analysis, impact analysis, or benefit risk analysis to take these benefits into account in the future.

Third, I set damage, searching, and control costs as a few fixed values under different control scenarios. However, these costs can vary over time. For example, the demand for timber is shown by the demand curve D. When timber is abundant, the supply of timber is shown by the supply curve S. Consumers can pay less (P) to obtain more timber (Q). When timber is scarce because of invasion, the supply curve of timber moves left (S'). Consumers need to pay more (P') and only obtain less timber (Q') (Fig.

54). In this case, the price of timber changes. This may case (1) land owners may not consider to execute control if $P' \times Q' \geq P \times Q$, or (2) I underestimate the value of damage.

Fourth, I represented the uncertainty in the initial population size with known distributions in different locations. Hence, future work could expand upon this to evaluate the scenario where land owners choose to monitor their lands even though the invasive species has not yet been found on their properties.

Fifth, allocation decisions occur between several management activities. The present study could be expanded to include other management activities. Several studies have discussed the prevention, control, and post-control, or trade stages (Olson and Roy, 2002; Costello and McAusland, 2003; McAusland and Costello, 2004; Olson and Roy, 2005), while the present study only focused on control and post-control stages. Combining these stages would capture broader situations facing not only land owners but also government agencies and nursery-related businesses, especially since the focused species of the present study still can be purchased at nurseries. This model applied to a single species, but land owners may address several species simultaneously. Future work could expand this model to include the evaluation of alternative priorities for land owners in allocating budgets or control efforts among various species.

4.5 Conclusions

Using an integrated model which included a logistic growth model, a diffusion model, and several economic elements, I estimated expected costs in forest productivity for Chinese tallow in East Texas and Louisiana and for Chinese and European privets

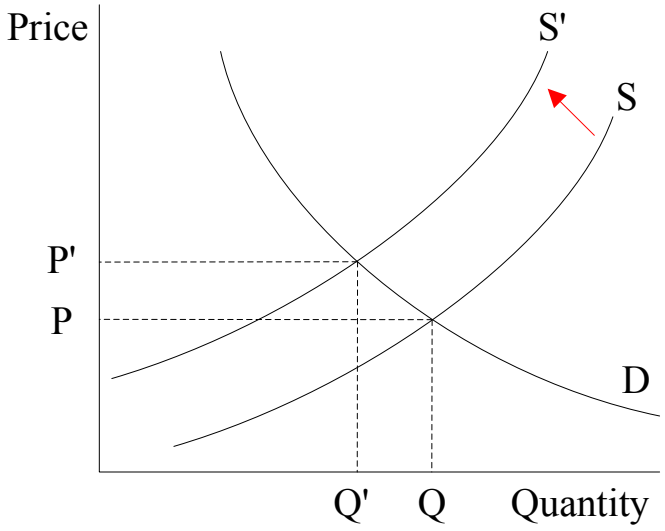

Fig. 54. Market allocation in timbers.

and Japanese honeysuckle in Mississippi and Alabama for five discount rates under four different control scenarios during the next 20 years. Twenty-year projections of the invasions of Chinese tallow in East Texas and Louisiana with no control, and under low, medium, and high control intensity indicated that the invaded area covered approximately 6.65×10^{6}, 2.45×10^{6}, 0.89×10^{6} and 300 acres. Expected costs in forest productivity between 1% and 9% discount rates with no control, and under low, medium, and high control intensity were 717-342, 631-315, 516-270, and 427-239 million dollars. Twenty-year projections of the invasions Chinese and European privets in Mississippi and Alabama with no control, and under low, medium, and high control intensity indicated that the invaded area covered approximately 3.81×10^{6}, 1.58×10^{6}, 0.52×10^{6} and 100 acres. Expected costs in forest productivity between 1% and 9% discount rates with no control, and under low, medium, and high control intensity were 3.68-1.88, 3.35-1.77, 2.72-1.51, and 2.34-1.38 billion dollars. Twenty-year projections of the invasions of Japanese honeysuckle in Mississippi and Alabama with no control, and under low, medium, and high control intensity indicated that the invaded area covered approximately 12.55×10^{6}, 2.96×10^{6}, 0.57×10^{6} and 300 acres. Expected costs in forest productivity between 1% and 9% discount rates with no control, and under low, medium, and high control intensity were 15.32-7.37, 11.70-6.22, 7.71-4.48, and 5.83-3.80 billion dollars. To decrease expected costs in forest productivity for these three invasions, high intensity control was recommended.

The merit of this study is that it represents integrating statistical forecasting approaches, ecological models, and economic concepts to project ecological invasions in

time and space under different control scenarios. As I mentioned before, the present model can be updated with the latest FIA data and modified by different management strategies, and the approach can be applied to other invasive species or locations. The model also explicitly represents, with an underlying probability distribution, the uncertainty associated with the initial size of an invasion. This is similar to the real world because government agencies often have to make decisions on controlling invasions without complete knowledge of invasion stage. Finally, I should say that economics cannot be the only measure of the worth of a species, nor the single method used to make decisions about ecosystem management. The present study suggests that an economic motivation can be addressed to social and ecological arguments for aggressively eliminating invasive species from the native forest lands that they have displaced over the last century.

5. CONCLUSIONS

Alien invasive species affect biodiversity, ecosystem function and services, and human health (Zavaleta, 2000; Kennedy *et al.*, 2002). The increased connectivity of the global human population has amplified the frequency and effect of biological invasions (Crowl *et al.*, 2008). Land-use and climate change, interacting with human transportation networks, also facilitate the spread of invasive species (Sakai *et al.*, 2001; Loewenstein and Loewenstein, 2005). Hence, there is a need to advance invasion ecology from a reactive science to a proactive science (Lodge *et al.*, 2006). This is because an important component of prevention and control of invasive species is the ability to forecast where and when invasion are most likely to occur initially, and where and when they are likely to spread.

I developed a novel methodology integrating statistical and mathematical approaches within a spatially-explicit simulation environment to forecast the spread of invasive species and to calculate the associated economic losses in forest productivity. The approach draws upon broad-scale, continuously updated, environmental and ecological survey data to address three specific questions. (1) Which areas are more vulnerable to invasion by exotic species? (2) Where, when, and how many invasions will occur? And (3) how much reduction in forest productivity will invasive species cause? This approach should be applicable to a variety of invasive plant species. I chose Chinese tallow, Chinese and European privets, and Japanese honeysuckle as focal species.

To determine which areas are more vulnerable to invasion by exotic species, I used logistic regressions to identify important landscape features which were correlated with invasions. This result improved the ability to predict which areas would be susceptible to invasion by a specific species, the potential effect on the local ecosystem, and what the most effective local control strategies would be. The implications of the results for monitoring and mitigating major invasive plant species are multifaceted. For example, given the most susceptible invasion sites, monitoring and mitigating efforts should target lands with low elevation; flat or gentle slope; close to water bodies and roads; damaged by animals, wind, or fire; recently harvested; and covered by young natural regeneration trees established with minimum site preparation. As the minimum temperature in winter plays a critical role in Chinese tallow invasions, this species could pose a much more severe threat to the southern U.S. forest with the predicted global warming.

To determine where, when, and how many invasions will occur, I used the results of the logistic regressions to parameterize logistic growth models and applied Fick's diffusion equation to develop dispersal models within an agent-based, spatially-explicit, simulation environment. This integrated approach along with a few improvements in the gathering of consistent data through time can provide managers with invasion information where and when these invasions might take place, so they can perform their jobs more effectively and efficiently. The long-term projections of these invasions also show an immense challenge for controlling these invasions and call for more aggressive policy actions in controlling this invasive plant species.

To determine how much reduction in forest productivity invasive species will cause, I applied economic concepts to simulate several control strategies. Linking economic concepts to the dispersal model provided an evaluation of different control scenarios that explicitly accounted for the spatial and temporal scales of the invasions. I reported specific expected costs related to forest productivity, but costs and benefits associated with ecological services were not available. The implications of these reports suggest high intensity control which needs holistic and coordinated efforts would be most cost-effective. Also, these reports can awake the public's attentions and motivate individuals for preventing and controlling invasions.

Invasive species management involves many concepts and careful consideration of projection methods. Even though the approach of the present study can be generally applied to other invasive plant species or locations, we still need to be aware that the uncertainty associated with forecasting a particular invasion using this model will vary depending on the spatial resolution, the species, and the stage of invasion. The detailed ecological study in several different areas will be needed for invasion distribution in the future, because we lacked the information on how specific species characteristics under different local conditions have affected biotic interactions in the past (Crowl *et al.*, 2008). In addition, there are several different factors that could potentially affect the rate of spread of a particular species, such as time since invasion, number and frequency of introductions, and population density (Jarnevich and Stohlgren, 2009). These factors are important components of any models of the distribution or abundance of a particular species in space and time, and need to be considered in the collection of field data.

Finally, the true challenge for future studies is to make policies and to educate public for preventing potentially harmful invasive species based on investigating the pros and cons of invasive species within a broader context.

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